

**Ciências
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**Dynamic soaring in the winds of change. The effects of wind and oceanography on
the population and spatial ecology of seabirds**

“Documento Definitivo”

Doutoramento em Biologia e Ecologia das Alterações Globais
Especialidade em Biologia e Ecologia Marinha

Francesco Ventura

Tese orientada por:
José Pedro Granadeiro
Paulo Catry

Documento especialmente elaborado para a obtenção do grau de doutor



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RESUMO

As aves marinhas são predadores de topo e são consideradas boas indicadoras das alterações ambientais dos ecossistemas dos quais dependem. Esta tese foca-se nas espécies de aves marinhas pertencentes à ordem Procellariiformes, as quais partilham entre si características demográficas semelhantes tais como uma elevada longevidade e uma maturação sexual tardia. Outra característica comum a muitas das espécies deste grupo é o facto de serem capazes de voar milhares de quilómetros nas suas viagens de alimentação, mesmo durante o período reprodutor (quando estão condicionadas a regressar à sua colónia com regularidade – *central place foraging*), tirando proveito da energia do vento através de um tipo de deslocação designado por “voo planado dinâmico” (*dynamic soaring*). O principal objetivo desta tese foi compreender os mecanismos através dos quais o vento e os processos oceanográficos afetam a demografia, a dinâmica populacional, a ecologia alimentar e a distribuição espacial das aves marinhas.

Utilizando o albatroz-de-sobrancelha (*Thalassarche melanophris*) como organismo modelo, desenvolvemos modelos populacionais integrados para estudar os efeitos do vento e de flutuações oceanográficas nas taxas de sobrevivência e de reprodução. Utilizando uma base de dados demográficos recolhida ao longo de cerca de duas décadas, descobrimos que os parâmetros reprodutores foram negativamente influenciados pela temperatura da superfície do mar, e positivamente afetadas pela intensidade do vento, o que pode estar relacionado com processos ambientais ascendentes (*bottom-up*) que determinam a disponibilidade e acessibilidade alimentar. A taxa de sobrevivência foi relativamente constante ao longo do período de estudo e foi apenas influenciada por alterações profundas no ecossistema que atuam a escalas espaço-temporais mais largas. Os nossos resultados revelaram também uma elevada sensibilidade da população para a taxa de sobrevivência de aves sub-adultas, que representam aproximadamente metade dos indivíduos da população, mas das quais se sabe muito pouco.

Estudamos de seguida a ocorrência de eventos de mortalidade não-relacionada com predação em crias de albatroz. Os resultados mostraram que, apesar das crias de albatroz terem uma massa inferior em anos com temperaturas do mar mais elevadas, a subnutrição e a regulação alimentar determinada pelas condições ambientais não explicaram os padrões de mortalidade observados. Detetámos, no entanto, um padrão de agregação espacial de pequena escala nos eventos de mortalidade não-relacionados com predação das crias de albatroz. Este resultado parece indicar que a variação inter-anual pronunciada no sucesso reprodutor dos albatrozes é modulada pela prevalência de uma doença infecciosa não identificada.

Através de modelos de espaço de estados (*state-space models*), quantificámos pela primeira vez uma hipótese anteriormente levantada, mas nunca documentada empiricamente – a da existência de um mecanismo que relaciona as condições ambientais com a reprodução numa população monogâmica. Descobrimos uma maior prevalência de divórcios em anos com condições mais adversas, caracterizados por temperaturas da superfície do mar mais elevadas. Este resultado documenta um efeito disruptivo direto do aumento da temperatura dos oceanos nos laços sociais monogâmicos dos albatrozes.

Focámos de seguida o estudo em duas espécies altamente móveis, a Freira do Bugio (*Pterodroma deserta*) e a Alma-negra (*Bulweria bulwerii*), utilizadas como organismos modelo para analisar o papel do vento no comportamento de voo e na ecologia alimentar de aves marinhas com voo planado dinâmico, durante o período reprodutor. As freiras do Bugio utilizaram ventos favoráveis para maximizar a sua velocidade de solo e a distância percorrida ao longo das suas viagens de

alimentação circulares, as quais estão entre as mais longas registadas em animais. Por outro lado, as almas-negras tiraram proveito dos ventos alísios do Atlântico Norte, exibindo uma elevada seletividade para ventos laterais, e movimentando-se em “zig-zag” ao longo de troços extensos do seu percurso. Esta estratégia permitiu às almas-negras, em condições estáveis de vento, maximizar tanto a distância percorrida como a probabilidade de detetar plumas de odor ao longo das suas viagens de alimentação. Os padrões de movimentos destas duas espécies indicam que as aves marinhas têm um conhecimento apriorístico das condições regionais do vento, e podem planear as suas viagens de alimentação com uma expectativa de encontrarem condições de vento (e consequentemente custos de voo) previsíveis no regresso à colónia.

No seu conjunto, os resultados da minha tese revelaram a sensibilidade das aves marinhas a alterações das condições oceanográficas, e a importância do vento para sustentar as características extremas das suas histórias de vida. Tendo em conta o ritmo acelerado das alterações globais e os seus efeitos dramáticos nos ecossistemas marinhos, monitorizar as respostas destas “sentinelas” do oceano global, e ser capaz de prever o seu desempenho futuro, devem ser vistos como objetivos fundamentais de conservação.

Palavras-chave

comportamento de voo, demografia, ecologia alimentar, ecologia do movimento, *Procellariiformes*

ABSTRACT

Seabirds are marine top predators regarded as indicators of the environmental changes occurring in their supporting ecosystems. The analytical lens of this thesis focusses on seabird belonging to the order *Procellariiformes*, which have similar life-histories characterised by high life expectancy and delayed sexual maturity. Furthermore, despite acting as central place foragers during breeding, most procellariiform seabirds can perform foraging trips covering thousands of kilometres by extracting energy from the wind through a flight behaviour known as "dynamic soaring". The overarching aim of my thesis is to understand the pathways through which wind and oceanographic processes affect the demography, population dynamics, foraging ecology and spatial distribution of seabirds.

Focussing on the black-browed albatross (*Thalassarche melanophris*) as a model organism, we developed integrated population models to investigate the effects of wind and oceanographic fluctuations on the population breeding and survival processes. By analysing a demographic database spanning nearly two decades, we found that the population breeding parameters were negatively impacted by higher sea surface temperatures and positively affected by stronger winds, presumably through bottom-up environmental processes modulating food availability and accessibility. Survival was relatively constant and was only influenced by deeper ecosystem changes acting at larger spatio-temporal scales. Furthermore, our results revealed the high sensitivity of the population to the survival rate of the poorly understood sub-adult life history stages, which comprised approximately half of the total population size.

We then studied the occurrence of albatross chick mortality events not caused by predation. Our results showed that, while albatross chicks weighed less in years with warmer sea temperatures, chick malnutrition and environmentally-driven food regulation did not explain the observed patterns of mortality. Rather, nestlings mortality events unrelated to predation were clustered at small scales in time and space, suggesting that part of the pronounced inter-annual variability in albatross breeding success was modulated by the prevalence of an unidentified infectious disease.

By developing state-space models, we quantified a previously hypothesised, but never empirically documented "habitat-mediated" pathway linking environmental conditions to the breeding processes of a social monogamous population. Specifically, we found a higher prevalence of divorce in challenging years characterised by warmer sea surface temperatures, documenting the direct disruptive effects of ocean warming on the social monogamous bonds of albatrosses.

Our work then focussed on the hypermobile Desertas petrel (*Pterodroma deserta*) and Bulwer's petrel (*Bulweria bulwerii*) as model organisms to investigate role of winds in shaping the flight behaviour and the foraging ecology of dynamic soaring seabirds during the breeding season. Desertas petrels used favourable winds to maximise their ground speed and distance covered throughout their round-trip foraging movements, among the longest recorded in any animal. Bulwer's petrels, on the other hand, exploited the stable North Atlantic trade winds, exhibiting a striking selectivity for crosswinds and engaging in crosswind zig-zag flight throughout large sections of their tracks. Under stable winds, this strategy enabled them to maximise the distance travelled and the probability of detecting odour plumes along the round trip. Crucially, the movement patterns of these two species suggest that seabirds have *a priori* knowledge of the regional winds and can plan their round-trip with an expectation of predicted wind conditions and costs of flight to return back to their colony.

Collectively, the findings of my thesis highlight the sensitivity of seabirds to changes in oceanographic conditions and their reliance on winds to sustain their extreme life-history. Given the accelerating pace of global change and its dramatic effects on marine ecosystems, monitoring the diagnostic responses of these "sentinels" of the global ocean and, crucially, predicting their future performance is a conservation goal of upmost importance.

Keywords

demography, flight behaviour, foraging ecology, movement ecology, *Procellariiformes*

CHAPTER 1

GENERAL INTRODUCTION

Aboard his ship at the mercy of a stormy Mediterranean Sea, Ulysses hears the Sirens and is awestruck and overwhelmed by their call. The origin of that call, which so fascinated and frightened the ancient mariners, was most likely the thousands of shearwaters returning by night to their breeding colony in an explosion of sound and life. The Sirens call is somewhat emblematic of the fascination that seabirds have always held over man. To the eyes of the ancient sailors, the mysterious seabirds effortlessly soaring over the towering waves were to all effects mythological creatures, embodying the wild and fierce spirit of the sea. In more recent times, and particularly so in the last few decades, the findings of seabird scientists shed some light on the ecology and life history of these animals. Yet, such advances in our ecological understanding of seabirds have by no means diminished our sense of wonder. On the contrary, as our knowledge ever increases, so too does our sense of wonder.

A unique window into the changing oceans

Before introducing the main ecological features of seabirds that make them particularly advantageous for addressing the focal questions of this thesis, I would like to begin this work by first outlining *why*, what the relevance of investigating the population and spatial ecology of seabirds is, in light of the unprecedented rate of environmental change of the Anthropocene. The global oceans are changing, suffering dramatic and ever increasing impacts driven by human activities and climate change (Poloczanska et al. 2013, Halpern et al. 2015, Jones et al. 2018, IPCC 2019). Due to the challenges of investigating processes taking place in the highly dynamic marine domain, our understanding of ocean ecosystems remains limited, posing an evident obstacle to the development of successful management and conservation actions. In this context, a precious source of information is represented by marine top-predators.

Owing to their apex position in the food web, marine top-predators are sensitive to changes across multiple trophic levels and are useful bioindicators of ecosystem health (Sergio et al. 2008). They play a fundamental role in structuring marine communities (Heithaus et al. 2008, Hazen et al. 2019) and exhibit population responses to environmental change and anthropogenic pressure (Sergio et al. 2008, Sydeman et al. 2015). In fact, due to their high sensitivity, many populations occupying high trophic levels in marine ecosystems are declining at an unprecedented rate (Heithaus et al. 2008). This is also true for seabirds, which are among the most threatened groups of vertebrates (Dias et al. 2019).

Seabirds are marine apex predators playing a critical role in the equilibrium of the world oceans, consuming every year a total biomass of the same order of magnitude as global fisheries (Parsons et al. 2008, Cury et al. 2011). Being wide ranging and long-lived, seabird populations play a critical "sentinel" role, responding to processes occurring over large, ocean-wide scales, and at a range of temporal scales (from seasonal to long-term climate variability) (Jenouvrier 2013, Iles & Jenouvrier 2019). During the breeding seasons, seabirds congregate in (often spectacularly large) breeding colonies, accessible to scientists, unlike most other marine predators. As a result, they have been the focus of extensive longitudinal ecological research, providing some of the longest and highest resolution time series data available to date. Thus, seabirds offer a uniquely advantageous viewpoint for monitoring and elucidating ecosystem change and the pathways through which

such change affects wild populations, with clear implications for management and conservation (Boyd & Murray 2001, Sergio et al. 2008).

The population and spatial ecology of seabirds

In this thesis, I focus on the population and spatial ecology of the pelagic seabirds belonging to the order *Procellariiformes*, also commonly known as the "tube-nosed" seabirds due to their characteristic external tubular nostrils. This order includes over 150 species comprising albatrosses, petrels, shearwaters, storm-petrels and diving-petrels, widely distributed across the oceans of the world. In this section, I briefly outline the life-history traits of seabirds, the main features of their foraging and movement ecology, and the role of wind and oceanographic processes in regulating their populations and spatial distributions.

Procellariiform seabirds have similar life-histories. They have high survival and life expectancy (with some species being exceptionally longevous), delayed sexual maturity and late age at first breeding, primarily thought to be necessary for immature individuals to attain the foraging skills of adult birds. All species are iteroparous and lay a single egg clutch at each reproductive attempt (Weimerskirch 2001). This demographic tactic, characterised by high survival and low fecundity, is considered an adaptation to the challenges of obtaining food in the marine environment (Ashmole et al. 1971). In fact, due to high survival rates and low natural predation, food availability is considered the key driver of seabird population dynamics and the regulation of seabird populations is mostly thought to be a bottom-up process linked to the oceanographic regulation of food supply (Ashmole 1963, Cury et al. 2011). In light of the variability in marine resources availability driven by oceanographic processes, seabirds evolved towards longer life spans, so that they can attempt reproduction over multiple years, but invest less in each single breeding attempt (Stearns 1976). Furthermore, it has been hypothesised and empirically documented in several studies that survival varies little between years, whereas fecundity is the trait mostly affected by environmental fluctuations (Sæther & Bakke 2000, Weimerskirch 2001, Forcada et al. 2008, Nevoux et al. 2010). Given their longevity and delayed maturity, the survival of adult individuals is predicted to be the main rate shaping the dynamics of seabird populations. However, a practical consequence of the delayed maturation is that substantial gaps of knowledge exist for the so-called "lost" years (Witham 1980), when juveniles and immatures are unobservable as they spend their first years of life at sea before returning to their breeding colonies (Hazen et al. 2012, Phillips et al. 2017).

Seabirds spend most of their lives on the wing in the open ocean, but, for a few months each year, they are tied to land to breed. They do so in large colonies, in which nesting individuals are relatively easy to observe, ring and manipulate. This, in turn, has made seabirds the focus of extensive ecological research, yielding high resolution individual-based datasets spanning decades. Overall, procellariiform seabirds were found to be highly faithful to their colonies of birth (philopatric), returning to their natal site to breed for the first time. Breeding adults are also generally highly faithful to their nesting site, often returning year after year to the very same nest or burrow (Gauthier et al. 2010, Campioni et al. 2017). Furthermore, as in many other avian species, seabirds are socially monogamous, forming long-term (and often life-long) bonds with their mates. Procellariiform seabirds, in particular, have remarkably low divorce rates, leading pairs to a high degree of mate familiarity and coordination, which is thought to be critical to provide enough food and successfully raise the young (Lack 1968, Ens et al. 1996, Bried et al. 2003).

During breeding, seabirds are central-place foragers (Stephens & Krebs 1986), periodically having to return to their nest to alternate incubation duties with their mate or attend and provision their chick. Yet, despite the central place constraint, they lead a wide-ranging highly pelagic lifestyle, often travelling thousands of kilometres to forage over immense ocean areas to find heterogeneously distributed prey, mostly consisting of various species of fish, crustaceans and mollusks (Granadeiro et al. 1998, McInnes et al. 2017, Waap et al. 2017) which they obtain on the sea surface or in the upper layer of the water column through shallow dives. The real extent of the seabird foraging range was poorly understood until the early 1990s, when the advent of tracking technologies revolutionised the study of animal movement, allowing for the tracking of individual seabirds (Jouventin & Weimerskirch 1990).

Tracking studies revealed that seabirds primarily adopt either a "commuting-type" or an "opportunistic-type" foraging strategy (Weimerskirch 2007). These different strategies are not only underpinned by the different species ecological characteristic (e.g. diet) and morphological adaptations (e.g. wing anatomy affecting flight performance), but also by the degree of predictability of their food resource. When adopting a "commuting" foraging strategy, birds leave their colony and direct their flight towards known foraging areas (often repeatedly targeting them along different foraging trips), thereby focussing their area-restricted-search (Kareiva & Odell 1987, Nevitt 2008). The existence of a commuting-type behaviour suggests that, at the large to meso-scale, pelagic seabirds can predict the presence of productive areas. The ocean is a tridimensional, highly dynamic, turbulent system, where ocean currents interacting with marine topography and other physical and biological processes shape the heterogeneous distribution of marine organisms (Haury et al. 1978, Bertrand et al. 2014). For instance, seabirds were found to exploit shelf-break or seamounts, known upwelling zones or dynamic oceanographic features such as eddies and fronts where prey concentration may be predictably higher (Weimerskirch 2007, De Pascalis et al. 2021). The "opportunistic" foraging strategy, instead, mainly consists of long, often looping trips, in which birds do not target specific areas but, rather, continuously search for food along the whole route and stop upon encountering a foraging opportunity. As the miniaturisation of tracking devices enabled for the tracking of smaller *Procellariiformes*, this opportunistic-type behaviour has been documented in several pelagic species feeding on more unpredictable food resources such as mesopelagic prey vertically migrating at night to the surface of the ocean (Clay et al. 2019).

As mentioned above, despite the central place constraint during breeding, procellariiform seabirds often carry out spectacular foraging trips, covering thousands of kilometres. These foraging movements challenge the main tenet of optimal foraging theory, according to which animals should minimise foraging costs whilst maximising their energy intake. The striking hypermobility of seabirds is underpinned by the flight behaviour known as "dynamic soaring" (Pennycuik 2002, Richardson 2011), with which many seabirds extract the energy for their long commutes from the wind, flying at negligible mechanical cost (Weimerskirch et al. 2000, Sachs et al. 2012). In recent years, thanks to the miniaturisation of tracking devices and to the ever increasing availability of concurrent wind data, it has been possible to perform detailed investigations of dynamic soaring, mostly targeting albatrosses, the "dynamic soarer" *par excellence*. When albatrosses soar, they extract energy from the wind by exploiting the wind velocity gradients ("wind-shear") close to the surface of the ocean. The typical flight pattern is an S-shaped manoeuvre, in which birds turn into the wind climbing up to 10-15 metres, banking and descending downwind across the wind-shear layer, to then turn upwind again and start a new cycle (Richardson et al. 2018). By adjusting the angles of their banked turns when carrying out

these consecutive swooping motions (beautifully described by writer Adam Nicolson as "the slow metronomic pulse of an ocean voyager's life"), albatrosses can move in virtually any direction relative to the wind, including directly upwind, without flapping their wings (Richardson 2011).

Thus, to minimise flight costs, dynamic soaring seabirds rely on the wind, which supports energetically efficient flight in some directions, but entails higher flight costs in others (Alerstam et al. 2019). Wind, and specifically the orientation bias relative to wind direction ("anemotaxis"), is therefore a crucial factor of efficient flight and has a major role in shaping the large-scale flight patterns and the movement ecology of seabirds (Weimerskirch et al. 2000, Wakefield et al. 2009). Most studies on the effects of wind focussed on the movements of large albatrosses tracked at high latitudes. However, compared to smaller species, albatrosses are less constrained in their choice of wind directions. Conversely, little is known about the effects of wind on the foraging movements of smaller procellariiform species. This knowledge gap is particularly evident for species inhabiting tropical and subtropical regions characterised by the persistent trade winds (Bernard et al. 2021). In these areas, birds gaining the benefits of tail winds when departing from the colony would have to pay the costs entailed by headwinds during the return flight, suggesting that in order to be efficient, their routes must be designed accounting for predicted flight performance along the round trip.

All these characteristics have long made *Procellariiformes* the model organisms to address fundamental ecological questions, such as the bottom-up regulation of population dynamics, the environmental effects on life history traits and the optimal foraging strategies for populations tied to a central place. In the next section, I introduce the study populations of my thesis and the features of their population and spatial ecology that make them particularly advantageous for testing ecological hypotheses and addressing the gaps of knowledge outlined above.

The study systems

The model organisms investigated in my thesis are three procellariiform seabirds: the black-browed albatross (*Thalassarche melanophris*); the Desertas petrel (*Pterodroma deserta*) and the Bulwer's petrel (*Bulweria bulwerii*).

Since 2003, around 400 black-browed albatross nests have been the subject of longitudinal monitoring on New Island, to the west of the Falklands/Malvinas archipelago (Catry et al. 2011). Over 70% of the world's black-browed albatrosses nest in the Falklands, and New Island is home to approximately 15500 black-browed albatross breeding pairs (Wolfaardt 2012). The data collected comprise: capture-mark-recapture data of each breeding individual and chick born in the study area; population counts; productivity (i.e. breeding success) data; and tracking data of foraging movements during incubation and breeding. In longevous species with delayed maturation such as albatrosses, the availability of long-term and comprehensive datasets is critical to investigate the demographic rates and population dynamics, particularly those of the "cryptic" life history stages such as juveniles and immatures. Individual-based datasets offer unique advantages for investigating the pathways through which oceanography and wind affect breeding and survival processes of long-lived and socially monogamous populations. By capitalising upon the information contained in such high resolution data, it is possible to test the predictions of the canalisation of life history traits theory, according to which the traits with highest impacts on the population fitness (in seabirds, the survival of adult individuals) should be buffered against environmental fluctuations (Nevoux et al. 2010). Moreover, in many socially monogamous species, divorce was found to be a behavioural mechanism triggered by previous breeding failure and aimed at improving the individual reproductive success with a new mate

(Culina et al. 2015). Therefore, as the environmental variability is predicted to primarily act upon the population productivity, this may in turn underpin an indirect link between environment and divorce driven by changes in demographic rates. However, whether the environment might also have a direct impact on divorce is largely unknown. Additionally, from a more applied perspective, an improved understanding of the population processes of this globally important population – which represents the only albatross population in the South Atlantic with a documented increasing trend (Wolfaardt 2012, Birdlife International 2018) – has clear implications for conservation. For instance, past anecdotal records (Tickell & Pinder 1975) suggested the occurrence of albatross chick mortality events for causes unrelated to predations, potentially indicating the prevalence of an infectious disease. However, whether these mortality events are driven by food availability or by an unidentified pathogen is presently unknown. As this source of mortality may significantly influence the population breeding success, addressing this gap of knowledge represents a conservation priority.

The other model organisms investigated in this thesis are the Desertas petrel and the Bulwer's petrel breeding in the Madeiran archipelago and in the archipelago of the Savage Islands, Portugal. In the past decade, the spatial ecology of both species has been the focus of research carried out using geolocation devices (Dias et al. 2016, Ramos et al. 2017) but their fine scale foraging movements and the effects of wind in shaping their spatial distribution remain poorly understood. Both species are specialist predators of mesopelagic prey, have wide foraging ranges and do not seem to consistently target specific hotspots of enhanced productivity or known foraging patches (Dias et al. 2016, Ramos et al. 2017). The striking motility of these petrels and their reliance on mesopelagic prey suggest that they may adopt an "opportunistic" foraging strategy based on an optimal use of wind to maximise distance covered and the probability of finding prey along the route (Weimerskirch 2007). The two species breed within the North Atlantic trade winds region, characterised by exceptionally persistent winds. Recent studies found that the hypermobility of these petrels may enable them to forage in areas both within and beyond the trade wind belt (Dias et al. 2016). In turn, this feature may provide sufficient environmental contrast to investigate the flight strategy adopted in stable winds or in areas with more variable winds. Furthermore, wind drives the dispersal of smells on the ocean surface, which should be particularly important for nocturnal seabirds. Thus, Bulwer's petrels, which are nocturnal predators spending over 90% of the night time in flight (Dias et al. 2015) should maximally benefit from the effect of wind in facilitating olfactory foraging. However, at present, the existence of optimal flight directions relative to wind across trade-offs of flight and olfactory search efficiency is poorly understood.

Importantly, the choice of advantageous study systems and the availability of long term and high resolution datasets are fundamental elements for the development of sophisticated and novel methodological approaches adopted in this work. The methodological advances presented here are an integral part of my thesis, and, as we discuss in the following chapters, can be widely applied to other study systems and ecological settings.

Objectives of this thesis

The overarching objective of my thesis is to understand the pathways through which oceanographic variability and wind affect the population processes and spatial ecology of Procellariiform seabirds. The specific research questions, outlined below, are the subject of manuscripts of scientific articles and are presented in the thesis chapter as follows.

Chapter 2. Demographic responses to environmental change of the black-browed albatross, sentinel of the Patagonian Shelf Large Marine Ecosystem

In this chapter, we focus on the demographic rates and population dynamics of a long-lived seabird, using the black-browed albatross as study system. By developing powerful integrated population models applied to our detailed longitudinal dataset, we investigate the environmental effects on the demographic processes of a longevous population, testing the predictions of environmental traits canalisation theory. Furthermore, we quantify the survival rate of the "cryptic" sub-adults life history stages and quantify the dynamics of the whole population. Specifically, the aim of the chapter is to investigate:

- i) What is the effect of candidate oceanographic covariates and wind on a long-lived seabird population survival and productivity process.
- ii) What are the demographic rates contributing to the population dynamics, and in particular how sensitive is the population to changes in the survival of juveniles.

Chapter 3. Spatial and temporal aggregation of albatross chick mortality events in the Falklands suggests a role for an unidentified infectious disease

Here, we focus on the albatross chick mortality for causes unrelated to predations. The occurrence of these mortality events are documented in previous studies, but the potential causes are currently unknown. We therefore ask:

- i) Are chick mortality events unrelated to predations underpinned by food availability of by an unidentified pathogen?
- ii) To what extent do these events impact the population breeding success?

Chapter 4. Environmental variability directly affects the prevalence of divorce in monogamous albatrosses

In this chapter, we use the longitudinal black-browed albatross database and focus on the occurrence of divorce events. In socially monogamous populations, breeding failures are thought to be the main trigger of divorce. As environmental fluctuations are predicted to primarily act upon the population productivity, this suggest the existence of an indirect link between environment and divorce, mediated by changes in demographic rates. However, "direct" pathways linking environment and divorce have not been documented in the ecological literature. Therefore, we ask:

- i) Do changes in oceanographic conditions and wind have a direct impact on the prevalence of divorce in a socially monogamous population?

Chapter 5. Gadfly petrels use knowledge of the windscape, not memorized foraging patches, to optimize foraging trips on ocean-wide scales

During breeding, despite being tied to a central place, seabirds cover vast distances in search for food. This impressive motility is made possible by the efficient use of wind to minimise the energetic costs of flight. However, little is known on how seabirds use winds, in combination with memory of foraging patches and adaptive search behaviour to exploit oceanic resources. To fill this knowledge gap, focussing on the pelagic Desertas petrels as model organisms, we ask:

- i) What is the role of wind in shaping the flight efficiency of a hypermobile central-place-foraging seabird population?

ii) How does wind affect the population foraging strategy and foraging range?

Chapter 6. Central place foraging seabirds fly at right angles to the wind to jointly optimize locomotor and olfactory search efficiency

In this chapter, we investigate the foraging movements of a nocturnal, small-sized seabird in the exceptionally persistent North Atlantic trade winds. Theoretical ecological studies suggest that, in stable winds, birds should fly at an orthogonal angle relative to the prevailing winds to optimise both the flight efficiency and the olfactory search, but this has not been supported by empirical data. Focussing on the Bulwer's petrel as model system, we test this theoretical prediction and ask:

i) Do nocturnal pelagic seabirds orient at a particular angle with respect to the wind to maximise the probability of detecting olfactory cues and therefore their olfactory foraging efficiency?

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CHAPTER 2

Demographic responses to environmental change of the black-browed albatross, sentinel of the Patagonian Shelf Large Marine Ecosystem

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ABSTRACT

In long-lived marine top-predators with delayed sexual maturity such as seabirds, adult survival is predicted to drive population dynamics. Major knowledge gaps exist for the cryptic sub-adult stages of the population. Yet as the oceans undergo dramatic change, investigating the trends of top-predator populations and their responses to environmental variability is key for a process-based understanding of climate change. Using integrated population models based on a longitudinal data set spanning nearly 2 decades, we investigated the demographic rates and environmental drivers shaping the dynamics of a longevous marine top-predator population, the black-browed albatross *Thalassarche melanophris* in the Falklands. We quantified the dynamics of the whole population, including its cryptic sub-adult stages, and examined the effects of candidate environmental covariates on adult survival and productivity parameters. We found that high survival rates of both adults and juveniles are the main contributors to the growth of this albatross population, the only one that is increasing in the South Atlantic. The breeding parameters were affected by environmental fluctuations through bottom-up processes, with a negative effect of higher sea surface temperatures and a positive effect of wind intensity. The relatively constant adult survival was influenced by deeper ecosystem changes, captured by large-scale indices (Southern Annular Mode). Approximately half of the total population is composed of sub-adults, and the population dynamics are highly sensitive to changes in juvenile survival; addressing current knowledge gaps in these cryptic life-history stages is therefore a conservation goal of primary importance.

Keywords

Juvenile survival; Demography; Integrated population model; Top-predator; Conservation; Seabird; Albatross

1. INTRODUCTION

Due to their apex position in the trophic web and high sensitivity to perturbation, top-predators are often regarded as reliable indicators of environmental processes occurring in their supporting ecosystems and are particularly useful in attracting the attention of a broader audience, given their inherent charisma and lever for public support for the conservation of biodiversity (Boyd & Murray 2001, Sergio et al. 2008). Marine ecosystems are being dramatically impacted by climate change (Poloczanska et al. 2013, Jones et al. 2018, IPCC 2019), but our understanding of these impacts remains limited. In this context, monitoring the population trends and demographic responses to environmental variability of marine top-predators allows for a unique analytical viewpoint for understanding the effects of climate change on wild populations and for promoting the conservation of biodiversity (Sergio et al. 2008, Hazen et al. 2019).

As top-predators, seabirds play a key role in the equilibrium of marine ecosystems (Parsons et al. 2008), consuming yearly prey biomass comparable to that of global fisheries (Cury et al. 2011). In seabirds and other longevous species with delayed maturity, adult survival is predicted to be the main demographic contributor to population growth and to be buffered against adverse environmental conditions (Sæther & Bakke 2000, Forcada et al. 2008, Nevoux et al. 2010a). Sub-adults — which we hereby define as individuals in the juvenile, immature and pre-breeding stages — are often unobservable as they spend their first years of life at sea before recruiting into their

breeding colonies (Phillips et al. 2017). Hence, due to the challenging nature of data collection for sub-adults and the key role of adult survival in shaping the dynamics of the population, substantial knowledge gaps exist for the cryptic sub-adult life-history stages (Hazen et al. 2012). Yet sub-adults often make up a substantial portion of the total population size, as estimated by Clay et al. (2019) and Carneiro et al. (2020) using age- and stage-structured matrix population models. Moreover, sub-adult birds are more vulnerable due to their inexperience (Gianuca et al. 2017). Thus, due to scarcity of information, the demographic contribution of the survival of sub-adult individuals to overall population dynamics is largely unknown.

Estimation of demographic parameters is a fundamental necessity for the development of mechanistic models and for process-oriented evaluation of population dynamics (Zipkin & Saunders 2018). A recent integrative modelling approach—using integrated population models (IPMs)—was developed to jointly analyse and capitalise on the strength of multiple demographic data sets (Abadi et al. 2010, Schaub & Abadi 2011), thus addressing the shortcomings of traditional separate analyses on survival, immigration and productivity. Compared to more conventional models that are applied to individual data sets, IPMs present a series of key advantages: proper error propagation by accounting for multiple sources of uncertainty and standardising the error structure across the different data sets incorporated in the model; increased precision of demographic estimates; and crucially, the capability of estimating hidden demographic parameters for cryptic life-history stages such as sub-adult stages in seabirds (Abadi et al. 2010, 2017, Schaub & Abadi 2011). IPMs have been utilised on mammals and other avian taxa (reviewed in Zipkin & Saunders 2018), but rarely in seabird population ecology studies (but see Véran & Lebreton 2008). Nevertheless, thanks to the accessibility of their breeding sites, several seabird species have been intensively monitored for decades, providing some of the best long-term ecological data sets available for the use of IPMs.

Here, we investigated the demographic responses of the black-browed albatross *Thalassarche melanophris* to environmental variability in the Falkland/ Malvinas Islands region. Albatrosses (Family Diomedidae) are among the most threatened seabird groups, and many populations worldwide are in steep decline (Birdlife International 2018a, Dias et al. 2019). In the South Atlantic, the only documented exception is, in fact, the increasing population of the Falklands black-browed albatross (Birdlife International 2018b). The objectives of our study were to:

- (1) investigate the Falklands black-browed albatross demographic rates underpinning the dynamics of the whole population, including the cryptic sub-adult life-history stages. We aimed to estimate the survival rate of juvenile birds (i.e. 1–3 yr old, see below) and quantitatively describe the full population structure by age-stage;
- (2) identify the main demographic contributors to population dynamics. In particular, we aimed to quantify the sensitivity of the population dynamics to the survival of juveniles;
- (3) examine the temporal variability of the adult survival and productivity processes and elucidate the effects of candidate environmental covariates on albatross adult survival and productivity parameters.

To achieve these objectives, we implemented Bayesian IPMs and a prospective sensitivity analysis framework, making use of the most extensive demographic and tracking data sets available for the Falklands albatross. These data sets comprised a longitudinal data set on population counts; high resolution (at a daily to weekly temporal resolution during the breeding season, see below) capture–mark–recapture (CMR) data; productivity data spanning 2005–2006 to 2019–2020

(hereafter, 2005–2006 will be referred to as the 2005 season, etc.) and GPS tracking data (2008–2019).

2. MATERIALS AND METHODS

2.1 Study system and available data

The Falkland Islands are home to the largest black-browed albatross population (over 70% of the global breeding population size), estimated at 475500 to 535000 pairs, distributed in 12 colonies across the archipelago (Wolfaardt 2012). The Falklands albatross population is mainly resident, foraging over the Patagonian Shelf Large Marine Ecosystem year-round (Ponchon et al. 2019). Food availability in the Patagonian Shelf is modulated by the Falklands/ Malvinas current, which originates from the Antarctic Circumpolar Current bringing cold and nutrient-rich waters to lower latitudes. The Patagonian Shelf is one of the most productive marine ecosystems in the world (Croxall & Wood 2002); it is a biodiversity hotspot of fundamental importance for regional economies and home to large populations of marine mammals and seabirds (Augé et al. 2018, Baylis et al. 2019), with a large portion of its avian biomass represented by black-browed albatross.

Our demographic study was based on New Island, to the west of the Falklands/Malvinas archipelago, where Catry et al. (2011) have been collecting high-resolution CMR data, population counts and productivity data. New Island is home to approximately 15 500 black-browed albatross breeding pairs. Incubation begins in October, hatching in the second week of December and fledging in April. The intensive CMR effort is based on daily (during incubation and brooding) and weekly (during post-brooding) visits to the study plots and their neighbouring areas. Thanks to the data collection protocol adopted (see Text S1 in the Supplementary Material), our data set also contains encounter histories of sub-adults that were ringed as chicks in our monitored plots and returned to the colony in the years prior to recruiting (Campioni et al. 2017), non-breeding adults and birds that emigrated from our study plots and recruited in the surrounding areas, collected on a daily to weekly basis. Every year, fieldwork started in the first days of October, prior to or at the onset of egg-laying, ensuring that the number of early failed breeders erroneously classified as non-breeders was minimal. This sampling strategy increased detectability rates, provided the IPM with recaptures of young and non-breeding birds and with explicit information on local immigration and emigration, thus improving the estimates of survival and breeding parameters. Our database comprised GPS tracking data from 2008–2019 (Text S1), which allowed for quantifying the areas of the southern Patagonian Shelf most intensively used by albatrosses using kernel utilization distributions (Worton 1989). The 90% contour of the kernel utilization distribution was used to define the relevant spatial domain for the extraction of the Patagonian Shelf environmental variables (Text S2). Recent DNA metabarcoding studies (McInnes et al. 2017a,b) revealed that the main dietary items of albatrosses breeding on New Island are fish (e.g. Fuegian sprat *Sprattus fuegensis* and rockcod *Patagonotothen* sp.) and crustaceans from the Family Munidae (lobster krill). To a lesser extent, their diet also includes scyphozoan jellyfish and cephalopods from the order Teuthida (squids). Due to the scarcity of information on prey distribution, we used environmental proxies for food availability and accessibility that may have affected albatross breeding and survival rates. Quantifying demographic responses to environmental variability is particularly challenging, as complex biological and oceanographic processes operate and interact at different spatio-temporal scales (Trathan et al. 2006). Here, we considered both fine-scale, short-lived proxies of the Patagonian Shelf physical and biological

variability and large-scale climate indices. Specifically: sea surface temperature anomalies (SSTAs), which we predicted to have a negative effect on albatross demographic rates; net primary production (NPP), which we predicted to have a positive effect; and mean wind intensity (WIND), predicted to have a positive effect. SSTAs, which are driven by atmospheric heat fluxes and vertical mixing, modulate (directly or indirectly) the recruitment and abundance of prey (Waluda et al. 1999, Arkhipkin et al. 2010). It has been shown that warm SSTAs negatively affect the breeding processes of other seabirds in the region, such as thin-billed prions *Pachyptila belcherii* from New Island (Quillfeldt et al. 2007). NPP — which is higher in colder, nutrient-rich waters — shapes the distribution of prey supporting pelagic seabirds, such as mid-trophic-level fish, squid and crustacean species (Chassot et al. 2010). WIND not only enhances water mixing and nutrient supply, thus having a positive effect on primary productivity, but can also reduce the commuting costs and hence the accessibility of foraging areas, particularly for dynamic soaring birds such as albatrosses and petrels (Ventura et al. 2020). The region is characterised by strong westerly winds, which are largely consistent in direction from one season to the next. This limited temporal variability in average wind direction is the reason why, in the analysis, we only considered mean wind intensity, which shows much more pronounced temporal variability. As we predicted that adult survival would exhibit limited responses to local environmental variability in the Patagonian Shelf, we also modelled adult survival as a function of the 2 dominant modes of climate variability in the Southern Ocean, captured by the large-scale climatic indices the Southern Annular Mode (SAM) and Southern Oscillation Index (SOI) (Forcada & Trathan 2009, Turner et al. 2009). To model the effects of large-scale climatic indices on albatross survival rates, we considered these indices under different temporal lags (Text S2) to capture the impacts at both short and long lags (Forcada & Trathan 2009). We hypothesised that the effects of environmental and climatic variables propagated (at different temporal scales, which we accounted for using different temporal windows for the variables extraction; see Text S2, Fig. S3) to the upper trophic levels, altering ecosystem structure, regulating food availability and, ultimately, affecting albatross productivity and survival processes.

2.2 Definition of the IPM

We constructed an age-stage structured Bayesian IPM with 12 age-stage classes (Fig. 1, Text S3) using a multi-event framework with a state-space modelling formulation for the CMR component, a state-space modelling formulation for the population count component and a binomial univariate regression for the productivity component. The IPM was structured as follows: fledglings (J_0) surviving to the first year (with juvenile survival probability, ϕ_j) move to the first juvenile age class (J_1); if they survive, they move to J_2 , then to J_3 and subsequently to the immature age class ('Imm', 4 yr old), all with ϕ_j . Once in this stage, immature birds acquire the same survival probability as adults (i.e. ϕ_a) (Nevoux et al. 2010b, Pardo et al. 2017a). If they survive to the following year, they enter the first pre-breeder stage ('PreB1', 5 yr old). Those that survive to the 6th year — which is the first year at which recruitment occurred in our study colonies—and recruit (i.e. breed for the first time, with probability of recruitment when 6 or 7 yr old ' recr_{6-7y} ') become either successful (S) or failed (F) breeders, with a first-time-breeder probability of success (i.e. of successfully fledging a chick) equal to ' succ_{PB} '. Those that do not recruit move to the 2nd and 3rd pre-breeder stages ('PreB2' and 'PreB3'), with probabilities of recruitment equal to ' recr_{6-7y} ' and ' recr_{8+y} ', respectively. Birds in PreB3 remain at this stage until recruitment. After recruitment, birds may breed annually with an adult probability of breeding (' breed_{adult} '; if not, they become non-breeders, 'NonB') and fledge a chick with an adult probability of success ' succ_{adult} ' (which we refer to as breeding success), becoming successful breeders, S (or failed breeders, F, if they attempt

breeding but fail to produce a fledgling). At each pre-breeder stage, surviving birds can emigrate and recruit outside of the study colonies with probability 'emig', thus entering the 'BreedOut' stage. Once birds are in the latter stage they are permanently out of the study cohort, an assumption that is consistent with 99% of the encounter histories of emigrating birds in our data set. In accordance with the states defined in our IPM, we hereafter define adults as birds that have attempted breeding at least once; sub-adults collectively refers to the juveniles, immature and pre-breeding stages and juveniles refers to birds 1–3 yr old, all characterised by the same survival probability, ϕ_j .

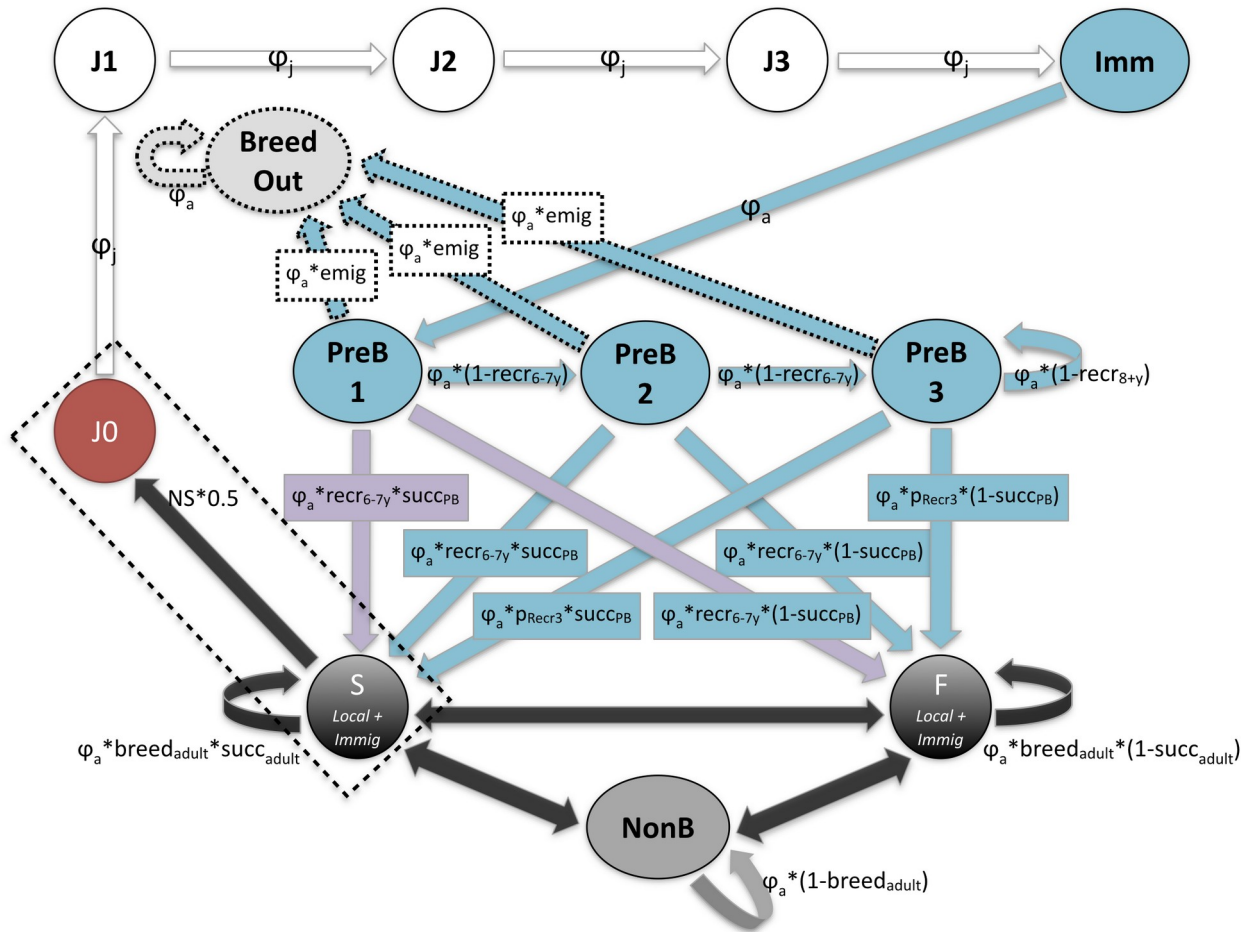


Figure 1 – The age-stage structured Integrated Population Model (IPM) describing the black-browed albatross population in New Island, Falklands. Different colours are used to visualise different detection probabilities: p_c (i.e. fledglings) in red; p_j (juveniles), in white; p_{ImmPB} (immatures and pre-breeders), in light blue; p_{BreedOut} (birds that emigrated and recruited outside), in light grey; p_{AdultB} (adult breeders), in black; $p_{\text{AdultNonB}}$ (adult non breeders), in dark grey. The states used to describe the albatross population are: fledglings (J0); juveniles of 1, 2 and 3 years of age (J1, J2, J3); immatures (Imm, 4 yr old); pre-breeders of 5, 6 and 7 years of age (PreB1, PreB2, PreB3); successful (S) or failed (F) breeders, including both the 'Local' birds that were born in the study cohort) and immigrant (Immig) adults that entered into our monitored plots as breeders; and non breeding birds (NonB), i.e. adult birds that skipped a reproductive attempt. At each pre-breeder stage, if birds emigrated and recruited outside of the study colonies, they entered the 'BreedOut' stage. See Table 1 for further parameter abbreviations.

2.3 Sensitivity analysis

As $\text{succ}_{\text{adult}}$ showed the highest inter-annual fluctuations (see Section 3.1 below), the 'reference' IPM adopted for the sensitivity analysis and for the description of the demographic rates and population dynamics (below) was the one accounting for temporal variability in $\text{succ}_{\text{adult}}$. Our framework was based on a prospective sensitivity analysis (Caswell 2000). The contribution of each parameter to future population growth (λ) was quantified by the changes induced by that parameter on λ (rather than focussing on the contribution of the observed variation in different demographic traits on the past changes in λ , which is the objective of a retrospective analysis). Starting from the last age-stage population counts (2019 season), we simulated future population dynamics (structured by age-stage) for the next 50 yr. Each year, the population trajectory was estimated by drawing each demographic parameter from a normal distribution with the same mean and standard deviation as the respective posterior distribution in the reference IPM, thus yielding a population matrix with 50 rows (the years) and 11 columns (the population age-stages). Simulations were repeated for 1000 iterations, generating 1000 population matrices. In each matrix, yearly λ was estimated by dividing the total population size at time-step $t + 1$ by the total population size at t ; λ was then estimated for each simulated matrix as the geometric mean of the yearly λ . Finally, the average λ and the 25–75% confidence interval were estimated, representing the reference λ calculated based on the same demographic parameter distributions estimated by the reference IPM. The sensitivity of λ to changes in each focal demographic parameter (e.g. ϕ_j) was estimated using the same analysis described above, but drawing the focal parameter (for example, ϕ_j) from a distribution with a mean decreased by $x\%$ (1, 2.5, 5 or 10%) compared to the mean of the parameter posterior distribution in the reference IPM, while the other parameters were kept as in the reference IPM. The sensitivity of λ (i.e. the % change of λ) to changes in the following demographic parameters was quantified: ϕ_a , ϕ_j , $\text{breed}_{\text{adult},t}$, $\text{succ}_{\text{adult}}$ and recruitment probabilities (i.e. simultaneous changes to both recr_{6-7y} and recr_{8+y}).

2.4 Analysis of temporal variability and effects of environmental variables

The demographic rates considered in this analysis were $\text{breed}_{\text{adult},t}$, $\text{succ}_{\text{adult}}$ and ϕ_a . After fledging, birds spend their first years of life at sea, leading to very few (if any) recaptures of birds aged 1–3 yr. As a consequence, the temporal variability in ϕ_j could not be estimated. The temporal variability of productivity ($\text{breed}_{\text{adult},t}$ and $\text{succ}_{\text{adult}}$) and ϕ_a was modelled by including each breeding season as a temporal random effect. Because of the complex IPM formulation, the temporal random effects on $\text{breed}_{\text{adult},t}$, $\text{succ}_{\text{adult}}$ and ϕ_a were separately included in 3 different IPMs (Text S3).

We then used univariate logistic regression to separately investigate the effect of the candidate covariates on ϕ_a , $\text{breed}_{\text{adult},t}$ and $\text{succ}_{\text{adult}}$. Due to the model complexity, it was not possible to reach model convergence if we tested for the effect of every variable on each parameter. Thus, we created a set of IPMs including either the Patagonian Shelf environmental covariates or the large-scale climatic indices. Prior to model fitting, we standardised the explanatory variables to facilitate model convergence. We used variance inflation factors (VIFs) from the 'AED' package in R (Zuur et al. 2009) to check that the variables included in each model were not collinear; in all models, the VIFs calculated for the explanatory variables were smaller than 2, indicating no collinearity. The effect of climatic indices on survival was tested using different time lags (Text S2). The importance of each covariate was assessed using inclusion probability parameters (O'Hara & Sillanpää 2009) (Text S3).

2.5 Model implementation

Analyses were performed using the JAGS software executed through R v.3.6.2 (R Core Team 2019) via the 'R2jags' package (Su & Yajima 2012), which uses a Markov chain Monte Carlo (MCMC)

algorithm to sample from the posterior distribution of each parameter in the model. For all models, we carried out the analysis generating 3 chains of at least 30 000 iterations. The chains were well mixed, and the Gelman-Rubin diagnostic convergence statistic (Brooks & Gelman 1998) was below 1.02 for all parameters, indicating that the chains converged adequately.

3. RESULTS

3.1 Demographic rates and population dynamics

The parameters $\text{breed}_{\text{adult}}$ and ϕ_a were considerably less variable than $\text{succ}_{\text{adult}}$ (Fig. 2). The demographic rates calculated by the reference IPM (Table 1), i.e. the one accounting for temporal variability in $\text{succ}_{\text{adult},t}$, revealed high ϕ_a (estimated at 0.94; 95% credible interval [CRI] = 0.936, 0.946) and ϕ_j (estimated at 0.75; CRI = 0.727, 0.789), as well as high $\text{breed}_{\text{adult}}$ (0.88; CRI = 0.872, 0.888) and $\text{succ}_{\text{adult}}$ (0.68; CRI = 0.545, 0.789). The temporal variance of breeding success (on logit scale) was estimated at $\sigma^2_{\text{succ}} = 1.04$ (CRI = 0.71, 1.97).

The estimated total number of black-browed albatrosses in our study (including individuals from all age classes at a given year, excluding chicks) increased from 724 (CRI = 585, 851) in 2005 to 1083 (CRI = 905, 1259) in 2019 (Fig. 3). Maximum population size of 1143 (CRI = 970, 1322) was recorded in 2015. During the entire period of the study, λ was 1.03 (CRI = 1.029, 1.035), with an average population increase of 3.3% yr⁻¹ (CRI = 2.49, 4.11). During the breeding season, adult birds (S, F and NonB) comprised the largest portion of the population (mean = 53.6%, range = 49.7–60.4%; these percentages and the ones below do not include chicks). On average, during the breeding season, adult birds (S, F and NonB) comprised 47.6% (range = 43.6–54.4%) and 6.1%, (range = 4.2–7.6%) of the total population size, respectively. Juvenile and immature birds made up, on average, 31.2% of the total numbers (range = 23.5–40.5%). Pre-breeders represented, on average, 15.1% of the population (range = 6.2–19.4 %).

3.2 Sensitivity analysis

Adult survival had the highest impact on the population dynamics (Fig. 4): a decrease of 1% in ϕ_a caused a 0.83% decrease in mean λ over the following 50 yr, leading to a yearly population decrease of 0.4%. Juvenile survival was the second most important contributor to population dynamics (Fig. 4). In particular, λ decreased by 0.19% as ϕ_j decreased by 1%. As ϕ_j decreased by 5 and 10%, λ decreased by 0.81 and 1.56% and the population size decreased by 0.38 and 1.14% yr⁻¹, respectively. A 1% decrease in $\text{breed}_{\text{adult}}$ and $\text{succ}_{\text{adult}}$ caused a reduction of 0.05 and 0.04% in λ , respectively. The sensitivity of λ to recruitment was marginal; in particular, a 1% decrease in the means of the distributions of both recruitment probabilities recr_{6-7y} and recr_{8+y} led to a 0.01% decrease in λ . In a simulated scenario in which the means of the recruitment probabilities distributions decreased by 99%, λ decreased by 2.55%, leading to a yearly population decrease of 2.4%, further suggesting the low sensitivity of growth rate to recruitment.

3.3 Effect of candidate covariates

Our results highlight a strong influence of local environmental conditions on the albatross productivity processes (Fig. 5). Hereafter, we use the Greek letter β to denote the regression slopes quantifying the effect size and 'w' for the inclusion probability parameters. The $\text{breed}_{\text{adult}}$ was significantly negatively affected by SSTA ($w > 0.99$, $\beta_{\text{SSTA}} = -0.20$, CRI = -0.26, -0.15; Fig. 5a) and, to a limited extent, by NPP ($w > 0.99$, $\beta_{\text{NPP}} = -0.17$, CRI = -0.23, -0.11; Fig. 5b). WIND ($w > 0.99$, $\beta_{\text{WIND}} = 0.11$, CRI = 0.06, 0.16; Fig. 5d) and NPP ($w > 0.99$, $\beta_{\text{NPP}} = 0.24$, CRI = 0.20, 0.28;

Fig. 5e) had a significant positive effect on adult breeding success, whereas SSTA had a negative effect ($w > 0.99$, $\beta_{SSTA} = -0.48$; CRI = -0.54 , -0.42 ; Fig. 5c). Conversely, ϕ_a was only marginally affected by local environmental covariates, and our IPMs only provided weak evidence for an inconclusive positive effect of WIND ($w \sim 0.80$, $\beta_{WIND} = 0.30$, CRI = -6.04 , 6.37). When we considered large-scale climate indices, there was a strong significant negative effect of SAM with a 1yr time lag on ϕ_a ($w > 0.99$, $\beta_{SAM} = -0.32$, CRI = -0.41 , -0.24 ; Fig. 5f), but not of SOI.

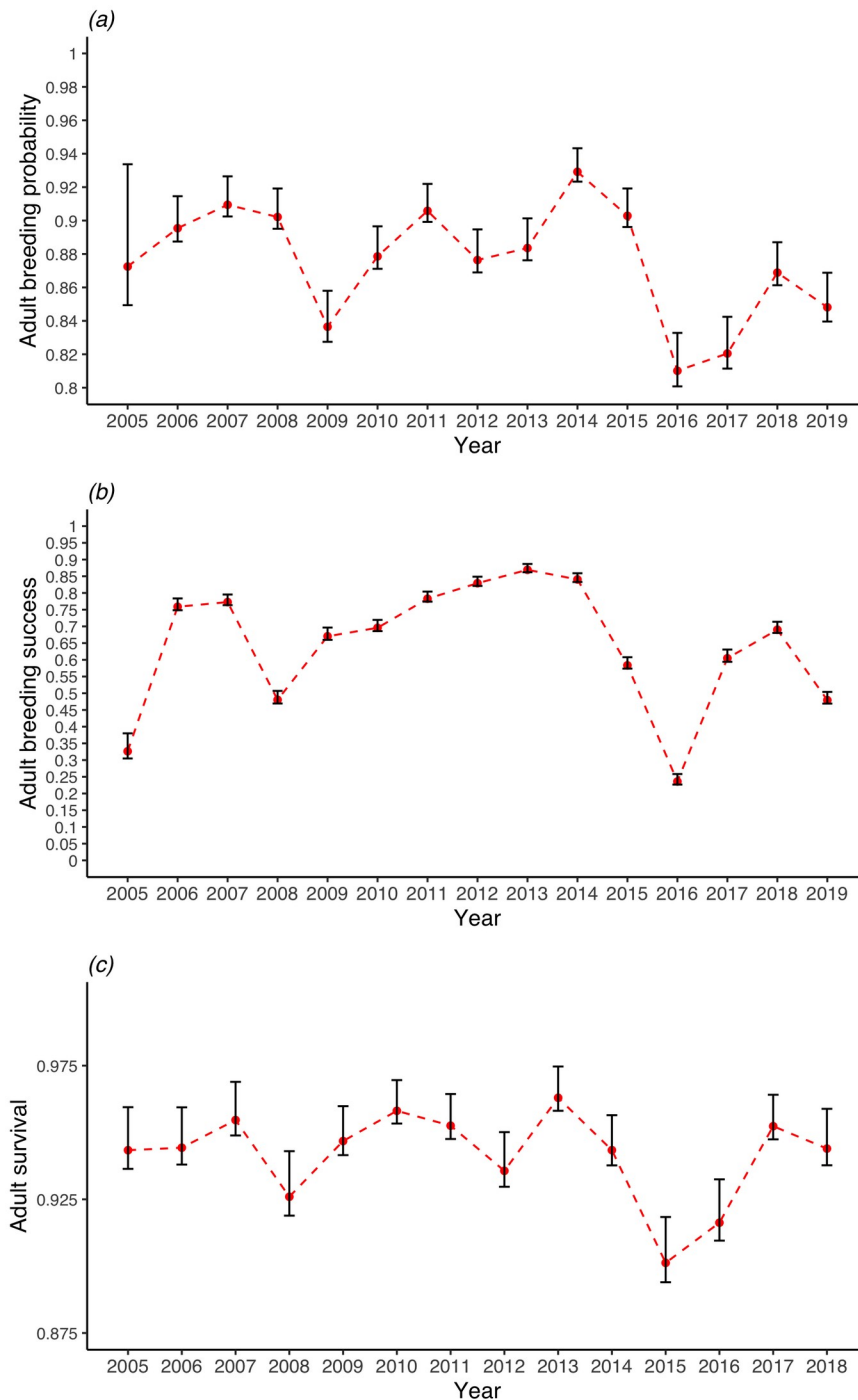


Figure 2 – Temporal variability of (a) breeding probability, (b) breeding success and (c) survival of adult black-browed albatrosses, estimated by the integrated population model. Dots: means; error bars: 95% credible interval (ranging from the 2.5th to the 97.5th quantile) of the parameter posterior distributions.

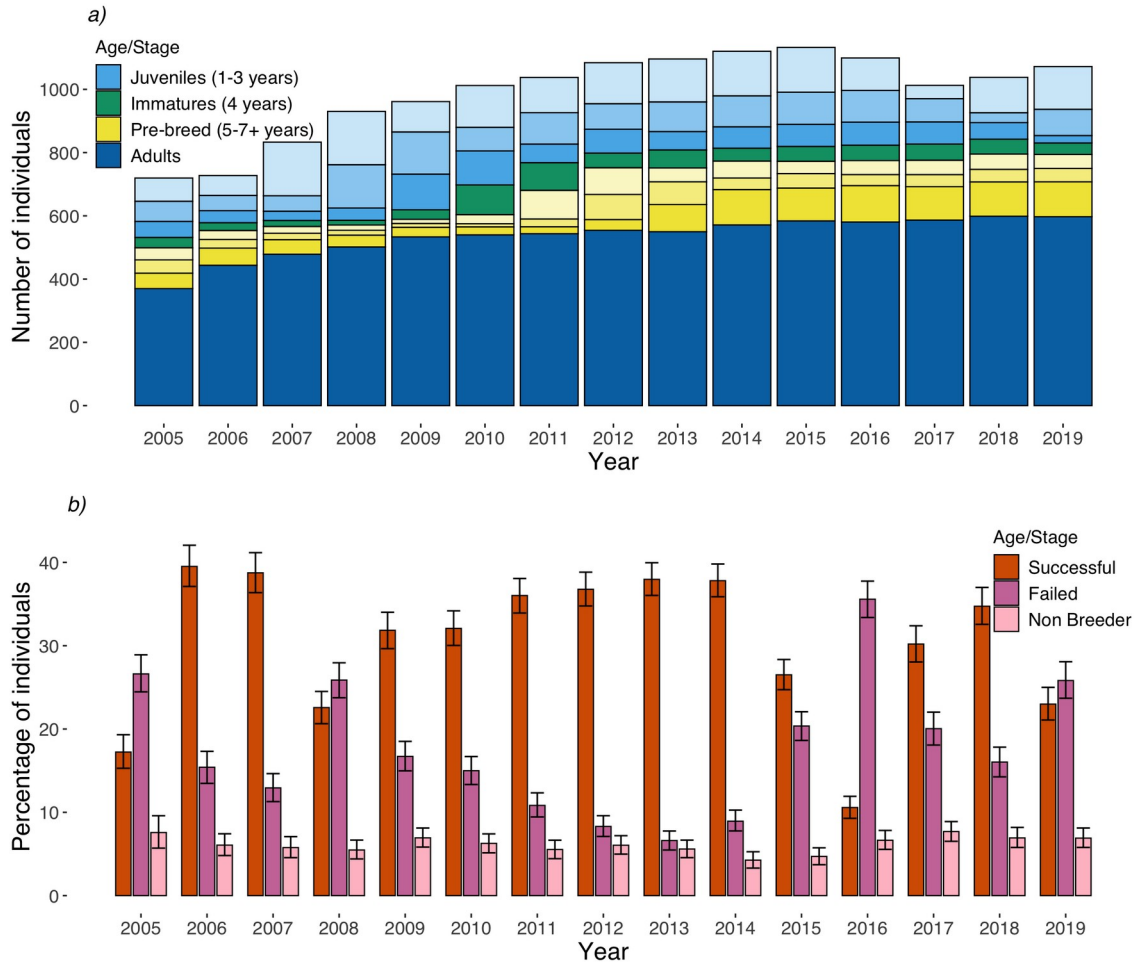


Figure 3 – (a) Number of black-browed albatrosses in each age-stage, each year, excluding chicks. Different shades of the same colour are used to represent different years of age within the same stage (for juveniles and pre-breeders, with the colours darkening as the birds get older). (b) The adult component of the population, with different colours depicting the percentage of successful, failed and non-breeding birds. Error bars: 95% credible intervals.

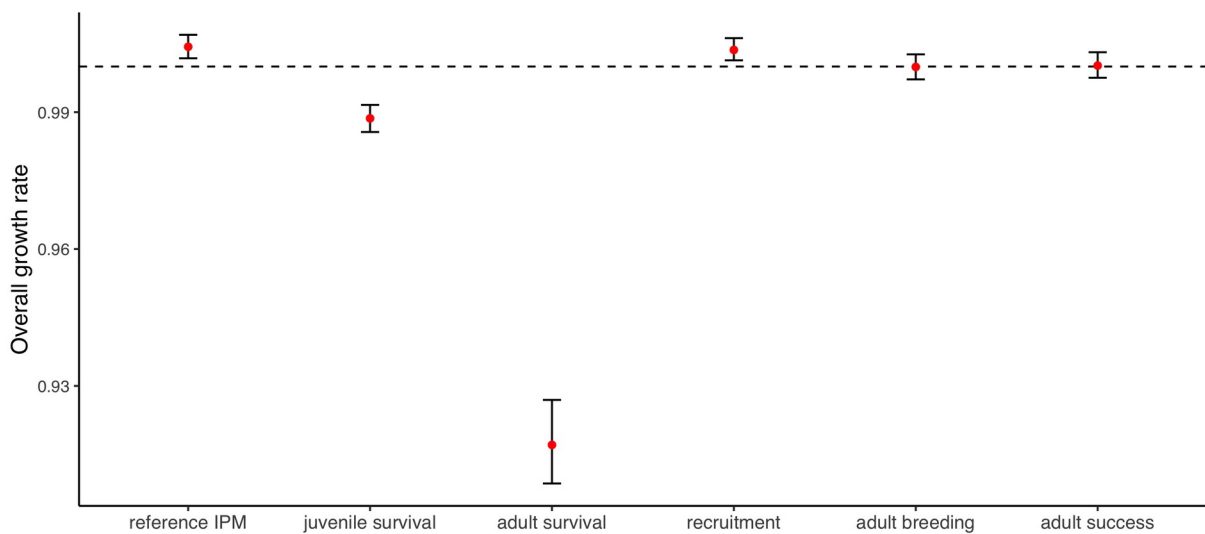


Figure 4 – Sensitivity of the overall black-browed albatross population growth rate to changes in the focal parameters juvenile survival, adult survival, recruitment rate, adult breeding probability and adult breeding success. The figure shows the overall population growth rate over the next 50 yr (y-axis) based on the unaltered 'reference' integrated population model (IPM; i.e. the one accounting for temporal variability in adult breeding success) and the overall growth rate as the mean value of each focal demographic parameter decreases by 10%. Dashed horizontal line: growth rate of 1 (i.e. a stable population). A growth rate below 1 indicates a population decrease. Dots: means; vertical error bars: 0.25, 0.75 quantiles.

Table 1 – The demographic parameters estimated by the "reference" Integrated Population Model, with temporal random effect on adult breeding success. As in this model adult breeding success varies temporally, we report the average success and its temporal variance on the logit scale. For each parameter, the 95% credible interval (CRI) ranges from the 2.5th to the 97.5th quantile of its posterior distribution.

Parameter	Mean (sd)	95% CRI
Juvenile survival (ϕ_j)	0.75 (0.03)	0.727, 0.789
Adult survival (ϕ_a)	0.94 (0.003)	0.936, 0.946
Probability of recruitment at year 6 or 7 (recr_{6-7y})	0.09 (0.01)	0.064, 0.112
Probability of recruitment at year 8 or above (recr_{8+y})	0.31 (0.03)	0.263, 0.352
Adult probability of breeding ($\text{breed}_{\text{adult}}$)	0.88 (0.005)	0.872, 0.888
First-time breeder probability of success (succ_{CPB})	0.40 (0.03)	0.339, 0.457
Adult average breeding success ($\text{succ}_{\text{adult}}$)	0.68 (0.07)	0.545, 0.789
Adult success temporal variance, logit (σ^2_{succ})	1.04 (0.48)	0.71, 1.97
Emigration and recruitment outside (emig)	0.31 (0.06)	0.241, 0.442
Chick detection probability (p_c)	0.99 (0.01)	0.96, 0.999
Juvenile year 1-3 recapture probability (p_j)	0.005 (0.001)	0.003, 0.006
Immature or pre-breeder recapture probability (p_{ImmPreB})	0.25 (0.02)	0.165, 0.275
Adult breeder recapture probability (p_{AdultB})	0.996 (0.004)	0.987, 1
Adult non breeder recapture probability ($p_{\text{AdultNonB}}$)	0.82 (0.03)	0.775, 0.864
Emigrated breeders recapture probability (p_{AdultOut})	0.35 (0.07)	0.118, 0.437

4. DISCUSSION

In this study, we provide among the first quantitative evaluations of the proportion of the total population size composed of sub-adults (juveniles, immatures and pre-breeders) in a long-lived

marine top-predator. Additionally, we robustly quantified the sensitivity of the population growth to changes in juvenile survival, a traditionally overlooked demographic rate. Direct quantitative links were established between the demographic rates of albatrosses and the environmental variability in their supporting ecosystem, which is information of particular value for assessing the impact of climate-related changes on long-lived top-predators. Our results were obtained through a widely applicable IPM framework, which is among the most refined demographic modelling methodologies and, at present, is underrepresented in the seabird literature despite its great potential for the analysis of longitudinal demographic data sets.

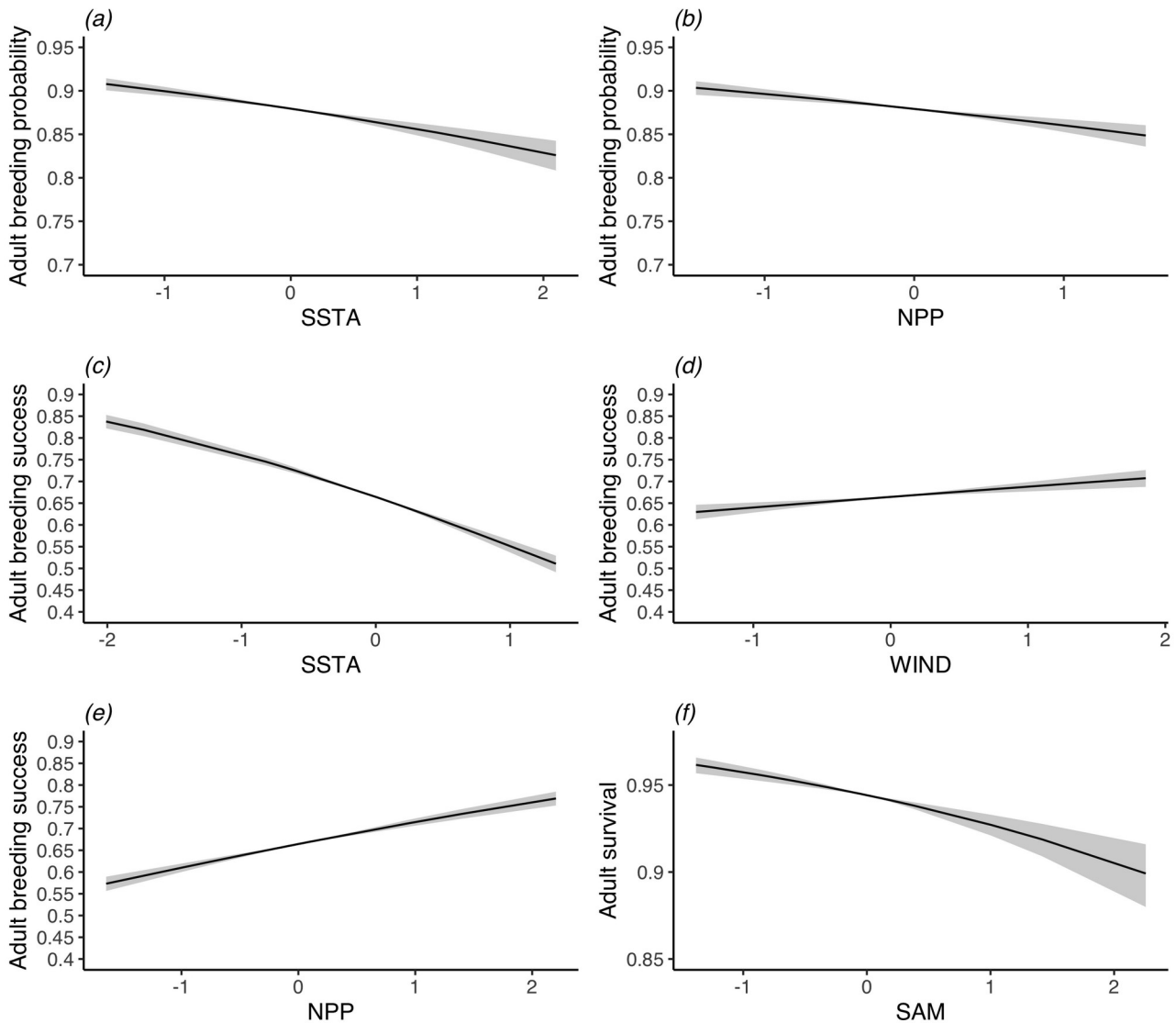


Figure 5 – The effect of (standardised) Patagonian Shelf environmental variables (sea surface temperature anomaly, SSTA; net primary production, NPP; wind intensity, WIND) and large-scale climate indices (Southern Annular Mode, SAM) on black-browed albatross productivity (breeding probability and breeding success) and survival parameters (adult survival). Shaded areas: 95% credible intervals.

4.1 Objective 1: Demographic rates and population dynamics

Given the global conservation importance of the Falklands black-browed albatross population, we provide a qualitative comparison of the demographic rates estimated in this study and those

computed (through non-integrated approaches) for other populations. As predicted for a species with high life expectancy (Gaillard & Yoccoz 2003, Forcada et al. 2008), we found high and relatively constant adult survival. In particular, the estimated ϕ_a (0.94) is higher than the estimates of other monitored black-browed albatross populations in South Georgia (0.88; Pardo et al. 2017a) and Kerguelen (0.91; Nevoux et al. 2010b). Together with high adult survival, the estimated ϕ_j (0.75) is also comparably high and in line with that of the Kerguelen population (0.78; Nevoux et al. 2010b) and higher than that of South Georgia over recent years (0.65; Pardo et al. 2017a). Moreover, the Falklands albatross population also had a high, relatively time-invariant $\text{breed}_{\text{adult}}$ (0.88), lower than the estimated rate for Kerguelen (0.96; Pardo et al. 2013) but higher than that of South Georgia (0.77; Pardo et al. 2017a). The estimated $\text{succ}_{\text{adult}}$ (0.68) was higher than the South Georgia estimate (0.3; Pardo et al. 2017a) and lower than the Kerguelen average rate for middle-aged ('optimal') birds (0.76, but this estimate was found to decrease significantly for younger and older animals; Pardo et al. 2013). In our population, $\text{succ}_{\text{adult}}$ was the most variable demographic parameter, ranging from 0.24–0.87; $\text{succ}_{\text{adult}}$ of experienced breeders was also the parameter with the highest temporal variability in Kerguelen and South Georgia, where it ranged from ~0.4–0.99 and from ~0–0.67, respectively (Nevoux et al. 2010a).

In albatrosses, as in other longevous iteroparous species, the survival of adult individuals is the trait with the highest sensitivity (see below) and it is therefore canalised against variability (Gaillard & Yoccoz 2003, Nevoux et al. 2010a, Hilde et al. 2020). Environmental disturbances on demography are therefore predicted to mainly affect productivity processes (Pons & Migot 1995, Oro et al. 1999, Thorne et al. 2015), with individuals investing less in reproduction and more in their own survival when conditions become harsher (Nevoux et al. 2010a). The high $\text{breed}_{\text{adult}}$ — and, despite its marked interannual variability, the relatively high $\text{succ}_{\text{adult}}$ — is therefore likely supported by the high food availability in the rich waters of the Patagonian Shelf, particularly compared to the collapsing population in South Georgia (Pardo et al. 2017a, Poncet et al. 2017), which is surrounded by less productive and more variable oceanic conditions (Nevoux et al. 2010a). Indeed, thanks to the more favourable conditions in the Patagonian Shelf, the sedentary Falklands albatross population was found to allocate proportionately more energy to feather synthesis while breeding compared to the albatrosses from South Georgia (Catry et al. 2013b), which are long-distance migrants in winter and experience harder conditions throughout their annual cycle (Rohwer et al. 2011, Catry et al. 2013b).

To the best of our knowledge, this is the first seabird study providing a strong estimate of the numbers of sub-adults and non-breeders based on a robust integrated approach. In this longevous population with delayed sexual maturity (a 'survivor' species at the slow end of the slow–fast continuum described in Sæther & Bakke 2000), the sub-adults (including juveniles, immatures and pre-breeders) represent a substantial part (just under half) of the whole population size. Hence, current knowledge gaps on the spatial and population ecology of these cryptic stages limit our understanding of the threats faced by such a large component of the whole population. In turn, this might critically hamper the design of effective conservation actions and mitigation measures in place for seabirds and other long-lived species with similar life histories (Clay et al. 2019, Carneiro et al. 2020).

4.2 Objective 2: Demographic contributors to population dynamics

In accordance with the predictions of life-history theory, the main demographic contributor to the observed population dynamics was adult survival. Our analysis also showed that the population dynamics were highly sensitive to changes in a critical demographic rate: the survival probability

of juveniles, ϕ_j . All other parameters being equal, our results showed that if ϕ_j decreased by 5%, the population would decrease at a rate of 0.38% yr⁻¹. This finding emphasises once again the urgent need to address the ecological knowledge gaps for these cryptic stages that likely face higher survival risk due to naïve foraging behaviours (Gianuca et al. 2017). To a minor degree, population growth was also sensitive to $\text{breed}_{\text{adult}}$ and $\text{succ}_{\text{adult}}$, whereas changes in recruitment probabilities only had a marginal effect on population dynamics. In the context of the observed decline of other albatross populations in the South Atlantic, our results shed light on the demographic drivers of the Falklands black-browed albatross population increase. Particularly compared to the population from South Georgia, the population growth seems to be underpinned firstly by the high survival probabilities of adults and juveniles and to a more limited extent by the high adult breeding probability and breeding success.

4.3 Objective 3: Temporal variability of productivity and survival

Overall, adult survival and, to a lesser extent, adult breeding probability were generally constant. Nevertheless, these parameters did show small interannual fluctuations. For a given year t , ϕ_a from t to $t + 1$ is significantly positively correlated with $\text{breed}_{\text{adult}}$ at year $t + 1$ (Pearson's correlation, $r_{12} = 0.85$, $p < 0.001$). This could be the consequence of 2 non-mutually exclusive processes. First, bottom-up environmental effects: when resources are plentiful (i.e. in 'good' years), survival throughout the previous (t) breeding and non-breeding season will be higher; in turn, more birds might attempt breeding in the following ($t + 1$) season, potentially facing reduced costs of reproduction owing to the more favourable conditions. Second, the mainly monogamous breeding strategy: if survival from the previous (t) to the following ($t + 1$) season is higher than average, adult breeders are more likely to reunite with their previous partners, which might in turn result in increased breeding probability in season $t + 1$.

The analysis of complementary data on the mean mass of chicks (Text S1) offered further insight into the survival and productivity temporal dynamics. Chick mass in season t was strongly positively correlated with $\text{breed}_{\text{adult}}$ and $\text{succ}_{\text{adult}}$ in the same season (Pearson's correlation, $r_{12} = 0.72$, $p = 0.004$; $r_{12} = 0.87$, $p < 0.001$, respectively) and with ϕ_a from season t to $t + 1$ (Pearson's correlation, $r_{11} = 0.69$, $p = 0.01$). The correlations between productivity and survival processes highlight the role of environmental conditions. During resource-poor seasons, adult birds respond by investing less in breeding; additionally, fewer of them breed successfully because of limited parental investment and less food availability (Pons & Migot 1995, Oro et al. 1999, Nevoux et al. 2010a). These detrimental conditions, which are potentially exacerbated by the higher costs of reproduction faced by those birds that did not defer breeding, ultimately leads to a reduction of adult survival.

Breeding success showed the most pronounced fluctuations across the study period. Together with the role of environmental drivers (further discussed below), a portion of the variability in $\text{succ}_{\text{adult}}$ might be caused by an unidentified infectious disease affecting albatross chicks, widespread in the albatross colonies across the Falklands, which can decrease breeding success by a minimum of 3.5% up to a maximum of 40% (Ventura et al. 2021).

Although ϕ_a was mostly constant, it suffered its sharpest drop in 2015, when it decreased from 0.94 (survival from the 2014 to the 2015 breeding season) to 0.90 (survival from the 2015 to the 2016 season). During this period, widespread marine megafauna mortality affected not only the black-browed albatross population, but also southern rockhopper penguins *Eudyptes chrysocome* and gentoo penguins *Pygoscelis papua* (Crofts & Stanworth 2017). Penguins, in particular, died in large numbers due to starvation (Crofts & Stanworth 2017). Anomalously low catches of Illex squid

Illex argentinus, which is one of the major contributors to the Falklands fishery revenue (Falkland Islands Government 2017), also evinced low productivity and food shortages. The results of our survival IPM suggest that the food shortages leading to this drop in survival might have been related to changes in the ecosystem structure and food chain associated with positive SAM phases (see below).

4.4 Objective 3: Environmental drivers of productivity and survival

Warm SSTA had a strong negative effect on $\text{breed}_{\text{adult}}$ and $\text{succ}_{\text{adult}}$. These matters are of concern in light of the current and predicted trends in sea temperatures (IPCC 2019) and the frequency of marine (Oliver et al. 2018) as a consequence of climate change. High SSTs, particularly in upwelling and frontal ecosystems, negatively affect primary and secondary production (Wilson & Adamec 2002, Behrenfeld et al. 2006, Barbraud et al. 2012), limiting food availability for seabirds through bottom-up mechanisms (Nevoux et al. 2010b, Barbraud et al. 2012, Sydeman et al. 2015, Pardo et al. 2017b). Our IPMs show that in cold and nutrient-rich waters, the higher NPP at the bottom of the food chain increases the availability of resources for higher level predators. Thus, during the breeding season, NPP positively affected $\text{breed}_{\text{adult}}$ and $\text{succ}_{\text{adult}}$. However, the result showing a negative effect of winter NPP on the $\text{breed}_{\text{adult}}$ is counter-intuitive (even if the effect size was weaker compared to that of SSTA). The non-breeding season (local winter) is characterised by low NPP, which might therefore be of limited significance in relation to food availability in this phase of the life cycle of the birds; rather, the negative effect of NPP might reflect potential interactions with biological or oceanographic processes unaccounted in our models. WIND positively affected $\text{succ}_{\text{adult}}$ (and also had an inconclusive positive effect on ϕ_a), suggesting its role in favouring food availability by enhancing convective water mixing, and also its direct effect on the accessibility of foraging patches by shaping the commuting costs. During breeding, seabirds act as central place foragers and undertake long foraging trips, reaching maximum flight effort (Ponchon et al. 2019) and often covering thousands of km (Ventura et al. 2020). During these trips they extract energy from the wind through a flight behaviour known as 'dynamic soaring' (Pennycuik 2002, Richardson 2011). Thus, wind conditions—especially wind intensity in areas where wind direction is relatively constant—shape the energy expenditure faced by commuting seabirds. In turn, this determines the spatial extent of the areas accessible for albatrosses to use and, ultimately, affects overall breeding success and, to a limited extent, adult survival. The non-significant effect of winter WIND on $\text{breed}_{\text{adult}}$ could be caused by the decreased flight effort (Ponchon et al. 2019) and increased opportunity to remain in proximity to good foraging patches during the non-breeding season.

SAM is the dominant mode of inter-annual climate variability in the Southern Ocean, affecting the ocean and atmospheric circulation and, most germane to this study, SSTs and primary productivity (Stenseth et al. 2003, Lovenduski & Gruber 2005). Positive SAM phases, which are predicted to become more frequent in the near future as a consequence of climate change (Turner et al. 2009, 2014), are associated with a contraction of the westerly winds towards the Antarctic, warmer SSTA and increments of downwelling events in the foraging domain of the albatross population (Lovenduski & Gruber 2005, Catry et al. 2013a, Ponchon et al. 2019). Adult albatrosses survival was strongly negatively correlated with SAM at a lag of 1 yr (Pearson's correlation, $r_{12} = -0.82$, $p = 0.0003$; Text S2, Fig. S4). This result is in agreement with the results of a recent study on Antarctic petrels *Thalassoica antarctica*, in which SAM (also considered at a 1 yr time lag) was found to negatively impact survival (Descamps et al. 2016). These studies suggest that SAM variability is associated with deep environmental changes affecting the ecosystem structure and

the whole trophic web (Stenseth et al. 2003, Lovenduski & Gruber 2005), ultimately having repercussions on the highly sensitive ϕ_a .

5. CONCLUSIONS

In this work, we provide a proof of concept on the fundamental importance of a process-based understanding in the demography of top-predator populations, only achievable through long-term monitoring. Thanks to the analytical depth attained by IPMs based on a comprehensive longitudinal data set, our study unravelled the mechanistic links between albatross demographic processes and environmental variability. We showed that black-browed albatrosses exhibit clear demographic responses to changes in their ecosystem, highlighting their role as sentinels of the Patagonian Shelf (Sergio et al. 2008). Our robust quantitative description of the structure of the albatross population shows that juveniles, immatures and pre-breeders comprise approximately half of the total number of individuals. Thus, addressing current knowledge gaps on these stages is of primary importance to design effective conservation measures. This is particularly true given our findings highlighting the sensitivity of the population to the (traditionally overlooked) survival rate of juveniles. Even with high adult survival rates, failing to encompass the young and inexperienced stages into well-designed conservation actions will likely prove to have serious repercussions on the overall population dynamics.

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SUPPLEMENTARY MATERIAL

Text S1. The available data

Demographic data

Since 2003, we collect capture-mark-recapture data, population counts and productivity data for the black-browed albatross (*Thalassarche melanophris*, hereafter BBA) population in New Island, Falkland/Malvinas Island. However, due to gaps in the chicks ringing data in 2004/05 (hereafter, 2004/05 will be referred to as the 2004 season, and so on and so forth) this study spans from the 2005 to the 2019 season. Birds ringed in 2003 and 2004 were assumed to enter the monitored study plots when they were first encountered after the 2004 season. Every year, we recorded all breeding birds nesting in 5 discrete sub-colonies and ringed every unringed breeder. The fate of each egg and chick was recorded daily (during the incubation and brooding phase) and weekly (during the post-brooding phase). Each chick surviving to the 60th day of age was ringed and considered as successfully fledged, as very few chicks die between this age and fledging. Chicks were weighed on the 58th and 60th day of age to obtain a robust estimate of their mass at 59 days old (average between the 58 and 60 days measurements). For each breeding season t , we calculated a yearly average chick mass (figure S1), which was significantly positively correlated with probability of breeding and breeding success in the same season (t) and survival from the current (t) to the subsequent ($t+1$) breeding season (see the main text).

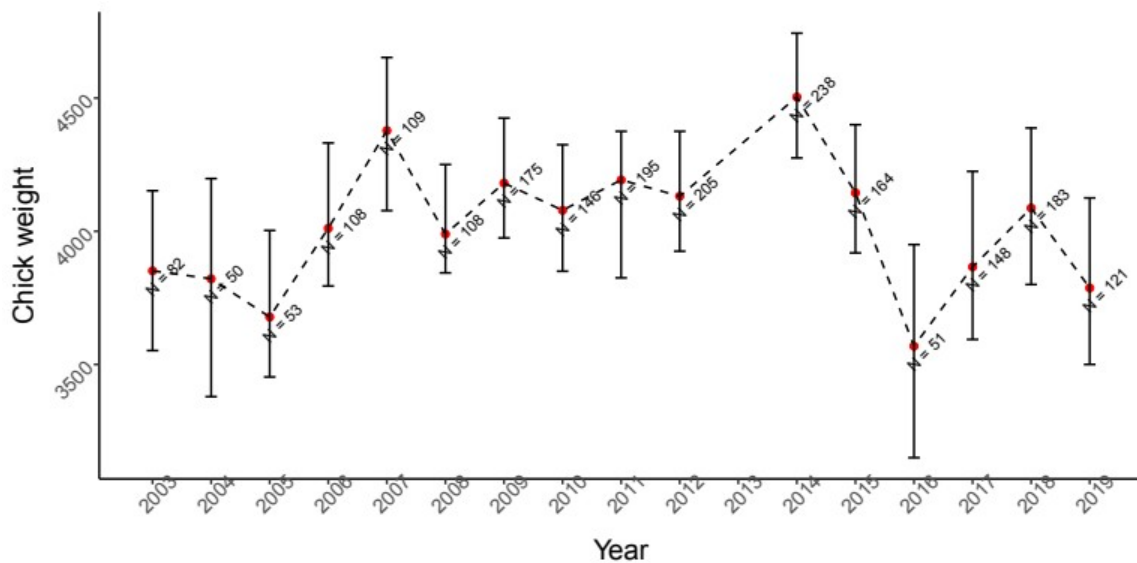


Figure S1. The yearly average chick mass at 59 days of age. The red circle represents the mean, the whiskers indicate the 25%-75% quantiles. Chick mass variability was positively correlated with probability of breeding and breeding success in the same breeding season, and with survival from the current to the following breeding season.

Throughout each study season, we recorded the identity of the ringed non-breeding birds seen inside and outside of our study patches; we also identified the ringed birds breeding outside the study colonies that were ringed as chicks in the study plots. Every year, we counted the number of individuals in each age-stage defined in the IPM; recorded the total number of breeders (dividing them into "local" breeders, ringed as chicks in our monitored plots, and "immigrant" breeders,

which entered the study cohort as breeding adults); and the total number of fledglings produced. The input data for the IPM is presented in table S1.

Table S1. Description of data input for the Integrated Population Model

Data Type	Description
Capture Mark Recapture	3173 individual encounter histories across 15 years. At each encounter event, each individual was assigned to one of the twelve age-stage classes defined in the IPM.
Population counts	Matrix 15 (years) × 12 (age-stage classes), storing the number of individuals recorded in each stage per year.
Productivity	Separate matrices for first-time-breeders and adult breeders. Each matrix is a 15 (years) × 2 (N fledglings, N breeding pairs) storing the number of fledglings produced per breeding pairs each year.

GPS tracking data

We collected GPS tracking data from breeding BBA on New Island during incubation (2009, 2013, 2017, 2018, 2019) and brooding (2008, 2009, 2010, 2013, 2015, 2016, 2017, 2018, 2019). GPS loggers were attached to the mantle and scapular feathers or to the tail feathers and set to record the bird location at a resolution of 7 or 14 minutes. The tracks were cleaned and the on-land and erroneous locations were removed. After processing, we obtained 735 foraging trips (157 and 578 during incubation and brooding, respectively). This represents the most comprehensive tracking dataset available for breeding BBA in the Falkland Islands.

Text S2. The explanatory variables

Estimate of space use for variables extraction

To reduce the computational burden of our dataset and make it treatable for the analysis, we adopted a resampling protocol. For each trip, we randomly resampled N points, separated from each other by at least 30 minutes, where N was equal to $2/3$ of the total trip duration in hours. In so doing, we reduced the intrinsic temporal autocorrelation of the dataset whilst rewarding longer trips with higher number of data points. Making use of the kernelUD function in the R package adehabitatHR (Calenge 2019), we calculated Kernel Utilisation Distributions (UD) based on the resampled tracks. The appropriate UD bandwidth was set as 30 km. The overall UD, estimated on a Lambert azimuthal grid centred in New Island, depicted the overall BBA space use (figure S2). The 90% contour of the overall UD was used to determine the spatial extent of the local oceanographic explanatory variables subsequently included in our IPMs (see below).

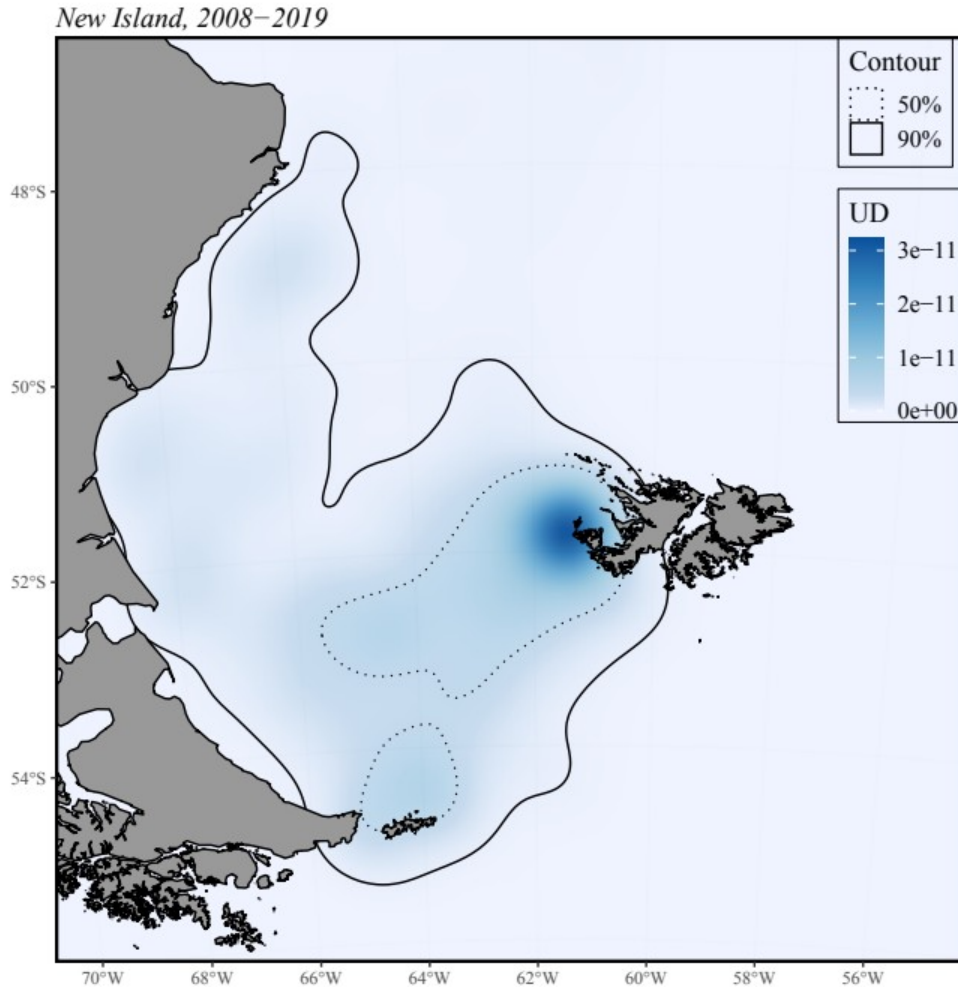


Figure S2. The overall Utilisation Distribution of black-browed albatross from the colony in New Island, Falkland/Malvinas Islands. Darker areas represent areas most intensely used by albatrosses. The 50% and 90% contours are showed with a dotted and solid line, respectively.

Explanatory variables extraction

We considered local oceanographic variables (sea surface temperature anomaly, "SSTA"; net primary production, "NPP"; wind intensity, "WIND"), extracted from the 90% contour of the overall UD; and large-scale climatic indices (Southern Annular Mode, "SAM"; Southern Oscillation Index, "SOI"). We hypothesised that local ocean variables could affect BBA adult survival (ϕ_a) and productivity (breed_{adult}, succ_{adult}) processes. As adult survival is the most sensitive trait in longevous species, we hypothesised that the variability in this parameter was influenced by deeper ecosystem changes, captured by large-scale indices. Hence, we included SAM and SOI as predictors for adult survival (ϕ_a).

The local oceanographic variables were Monthly Multi-scale Ultra-high Resolution SSTA (°C), downloaded from NOAA at a spatial resolution of 0.01° (<https://coastwatch.pfeg.noaa.gov/erddap/griddap/jplMURSST4.1anommday.html>). Remotely sensed NPP (mg/m²) rasters, produced by Copernicus Marine Environment Monitoring Services (<https://oceansci.gsfc.nasa.gov/MODIS-Aqua>), were downloaded at a spatial resolution of 0.04° and daily temporal resolution, but were subsequently summarised as monthly averages for every month in the study. WIND (m/s) was calculated from wind meridional and zonal components reanalysis available from the ECMWF ERA-5 database

(<https://cds.climate.copernicus.eu/cdsapp>), at a spatial and temporal resolution of 0.25° and 6 hours. Monthly mean WIND rasters were calculated for each month in the study.

The SAM index, available on the British Antarctic Survey database (<http://www.nerc-bas.ac.uk/icd/gjma/sam.html>) is the atmospheric pressure difference between the latitudes 40°S and 65°S . SAM is the main mode of inter-annual climate variability in the Southern Hemisphere, deeply influencing the circulation (winds, sea surface temperatures and chlorophyll concentration) on the Patagonian Shelf and in the Southern Ocean (Lovenduski & Gruber 2005). SOI was downloaded from <http://www.cpc.ncep.noaa.gov/data/indices/soi>. It is calculated as the difference in surface air pressure between Tahiti and Darwin and captures large-scale fluctuations in air pressure across the tropical Pacific. Negative SOI phases indicate El Niño years, with anomalously warm ocean waters and a dramatic reduction in nutrients availability across the eastern tropical Pacific (Barber & Chavez 1983, Cai et al. 2014).

Both local oceanographic variables and large-scale indices were averaged across three observation windows (figure S3), considered the relevant time spans during which the explanatory variables affected the demographic parameters in exam. For $\text{breed}_{\text{adult}_t}$, the variables were averaged across the wintering season (i.e. from april to september) prior to the focal breeding season; for $\text{succ}_{\text{adult}_t}$, the selected window comprised the focal breeding season, from october to march; for ϕ_a , the variables were averaged from october (i.e. the beginning of the focal breeding season) to september (i.e. the end of the subsequent wintering season). For the large-scale indices, we hypothesised that a lag was required for their effects to reach the upper trophic levels and affect BBA demography, particularly for the El Niño anomalies that need to propagate and be transferred to the South Atlantic (Stenseth et al. 2003). We therefore tested their inclusion under different temporal lags: 6, 12, 24 and 36 months for SAM; and 12, 24 and 36 months for SOI. The temporal lags were applied to the survival temporal window (october to september). The only large-scale index retained as significant in our IPMs was SAM, with a lag of 12 months (figure S4).

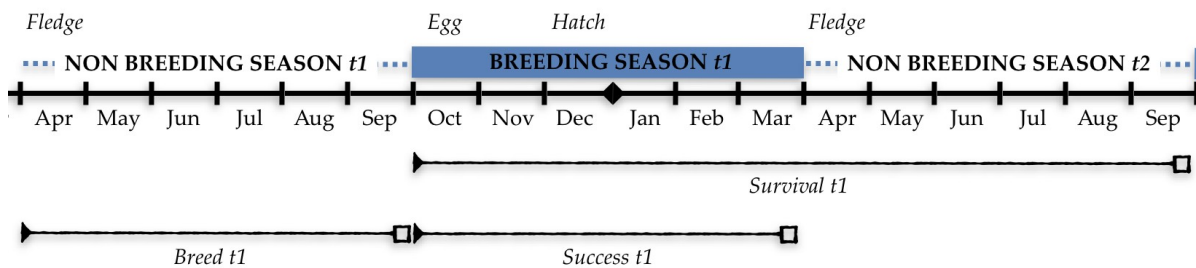


Figure S3. The observation windows considered for the extraction of the explanatory variables in our models. For the focal season t_1 , the relevant time-span for the probability of breeding was the non-breeding season before ($Breed\ t_1$, april to september t_1). For breeding success, the selected time-span was the focal breeding season ($Success\ t_1$, october to march t_1). The observation window considered for adult survival was the focal breeding season to the end of the subsequent non-breeding season ($Survival\ t_1$, october t_1 to september t_2).

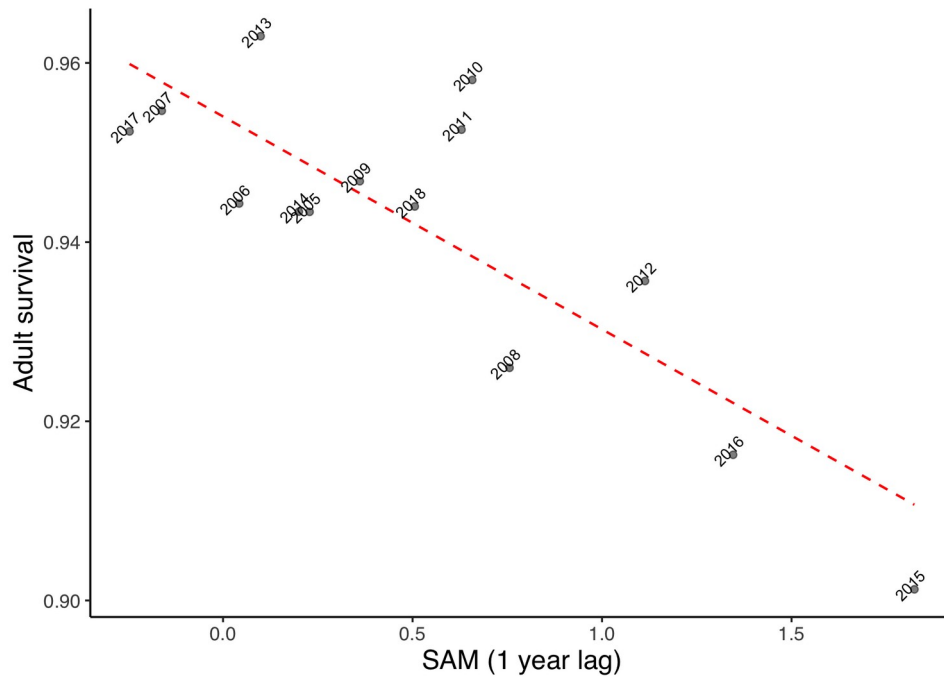


Figure S4. The correlation between adult survival and SAM averaged across the survival temporal window (October to September) with a time-lag of 1 year. Adult survival was strongly negatively correlated with SAM (Pearson's correlation, $r_{12} = -0.82$, $P = 0.0003$). SAM with a lag of 1 year was the only variable retained in the survival IPM.

Text S3. The Integrated Population Modelling framework

Background

Changes in population size over time are driven by demographic rates. The link between population processes (parametrised by demographic rates) and the outcome of these processes (i.e. the population abundance) is straightforward:

$$N_{t+1} = N_t * f(S, P)$$

where N is the population size and f is a generic function of survival (S) and productivity (P). Time-series datasets on abundance therefore intrinsically contain information about the underlying demographic processes. However, traditionally, studies focusing on population dynamics often estimate abundance, survival, fecundity and other demographic rates by separately analysing different type of datasets. In turns, this hampers our understanding of the whole set of processes shaping the changes in population size.

The integrated population models (IPMs) are a novel, powerful tool developed to simultaneously analyse various type of demographic data into a unified modelling framework (Abadi et al. 2010, Schaub & Abadi 2011, McCaffery & Lukacs 2016). IPMs jointly analyse time series of counts; data on demographic rates such as individual based capture-mark-recapture datasets; and data on productivity. In so doing, IPMs capitalise on the strengths of each dataset to yield better estimates of population trajectories. Furthermore, by extracting information for a parameter of interest from multiple data sources, IPMs estimate demographic rates with increased precision compared to conventional models applied to separate datasets. In particular, IPMs proved to be particularly effective in estimating critical parameters difficult to quantify due to the lack of

explicit information. Moreover, the flexibility of the IPM formulation allows for modelling the effects of candidate covariates of interest on specific demographic parameters.

IPM formulation

We constructed an age-stage structured IPM with twelve age-stage classes (described in the "Materials and Methods" section in the main text). We adopted a state-space modelling formulation to model the population count (Kéry & Schaub 2012b a) component of the IPM. Since in the IPM population counts inform demographic rates and vice-versa, failing to capture emigration would lead to underestimates in the survival parameters. Conversely, not accounting for the immigration process (through which immigrating successful or failed breeders first enter into the study cohort) would yield inflated estimates of breeding parameters and adult survival. To account for emigration, we incorporated the *BreedOut* stage into the IPM using data on birds ringed as chicks in our study plots that were subsequently recaptured outside. To capture the immigration process, we used data on local (i.e. which were born in the study cohort) and immigrant adults (i.e. which entered into our monitored plots as breeders). The number of immigrant breeders was simply added to the state equations describing the successful and failed breeders dynamics; in so doing, the demographic parameters only shaped the local component of the breeding population.

The following set of state equations was used to describe the dynamics of the true, but unknown, age-stage population sizes over time. In order to account for stochasticity, we used the Poisson (Po) and Binomial (bin) statistical distributions. To model the number of chicks at each time-step t , we used a Poisson distribution with rate equal to $0.5 * N_{S,t}$ (i.e. half of the total number of successful breeders at the same time-step).

$$N_{J_0, t+1} \sim \text{Po}(0.5 * N_{S, t+1})$$

$$N_{J_1, t+1} \sim \text{Po}(N_{J_0, t} * \phi_j)$$

$$N_{J_2, t+1} \sim \text{bin}(\phi_{j_r}, N_{J_1, t})$$

$$N_{J_3, t+1} \sim \text{bin}(\phi_{j_r}, N_{J_2, t})$$

$$N_{Imm, t+1} \sim \text{bin}(\phi_{j_r}, N_{J_3, t})$$

$$N_{PreB_1, t+1} \sim \text{bin}(\phi_{a_r}, N_{Imm, t})$$

$$N_{PreB_2, t+1} \sim \text{bin}(\phi_{a_r}, N_{PreB_1, t} * (1 - \text{regr}_{6-7y}))$$

$$N_{PreB_3, t+1} \sim \text{bin}(\phi_{a_r}, (N_{PreB_2, t} * (1 - \text{regr}_{6-7y}) + N_{PreB_3, t} * (1 - \text{regr}_{8+y})))$$

$$N_{BreedOut, t+1} \sim \text{bin}(\phi_{a_r}, (N_{PreB_1, t} * \text{regr}_{6-7y} * \text{emig} + N_{PreB_2, t} * \text{regr}_{6-7y} * \text{emig} + N_{PreB_3, t} * \text{regr}_{8+y} * \text{emig}))$$

$$N_{S, t+1} \sim \text{bin}(\phi_{a_r}, (N_{PreB_1, t} * \text{regr}_{6-7y} * (1 - \text{emig}) * \text{succ}_{PB} + N_{PreB_2, t} * \text{regr}_{6-7y} * (1 - \text{emig}) * \text{succ}_{PB} + N_{PreB_3, t} * \text{regr}_{8+y} * (1 - \text{emig}) * \text{succ}_{PB} + (N_{S, t} + N_{F, t} + N_{NonB, t}) * \text{breed}_{adult} * \text{succ}_{adult})) + N_{SImmig, t+1}$$

$$N_{F, t+1} \sim \text{bin}(\phi_{a_r}, (N_{PreB_1, t} * \text{regr}_{6-7y} * (1 - \text{emig}) * (1 - \text{succ}_{PB}) + N_{PreB_2, t} * \text{regr}_{6-7y} * (1 - \text{emig}) * (1 - \text{succ}_{PB}) + N_{PreB_3, t} * \text{regr}_{8+y} * (1 - \text{emig}) * (1 - \text{succ}_{PB}) + (N_{S, t} + N_{F, t} + N_{NonB, t}) * \text{breed}_{adult} * (1 - \text{succ}_{adult}))) + N_{FImmig, t+1}$$

$$N_{\text{NonB}, t+1} \sim \text{bin}(\phi_a, (N_{S,t} + N_{F,t} + N_{\text{NonB},t}) * (1 - \text{breed}_{\text{adult}}))$$

The observation equations linked the true states to the observed data by accounting for age-stage specific probability of detection: p_C (i.e. nestlings detection probability); p_J (juveniles); p_{ImmPB} (immatures and pre-breeders); p_{BreedOut} (birds that emigrated and recruited outside of the study colonies); p_{AdultB} (adult breeders, both successful and failed); $p_{\text{AdultNonB}}$ (adult non breeders).

$$Y_{J_0, t} = N_{J_0, t} * p_C$$

$$Y_{J_1, t} = N_{J_1, t} * p_J$$

$$Y_{J_2, t} = N_{J_2, t} * p_J$$

$$Y_{J_3, t} = N_{J_3, t} * p_J$$

$$Y_{\text{Imm}, t} = N_{\text{Imm}, t} * p_{\text{ImmPB}}$$

$$Y_{\text{PreB1}, t} = N_{\text{PreB1}, t} * p_{\text{ImmPB}}$$

$$Y_{\text{PreB2}, t} = N_{\text{PreB2}, t} * p_{\text{ImmPB}}$$

$$Y_{\text{PreB3}, t} = N_{\text{PreB3}, t} * p_{\text{ImmPB}}$$

$$Y_{\text{BreedOut}, t} = N_{\text{BreedOut}, t} * p_{\text{BreedOut}}$$

$$Y_{S, t} = N_{S, t} * p_{\text{AdultB}}$$

$$Y_{F, t} = N_{F, t} * p_{\text{AdultB}}$$

$$Y_{\text{NonB}, t} = N_{\text{NonB}, t} * p_{\text{AdultNonB}}$$

The likelihood for the age-stage population count data is the product of the likelihood of the observation and process equations, and is denoted as:

$$L_{\text{COUNT}}(y \mid \phi_a, \phi_j, \text{recr}_{6-7y}, \text{recr}_{8+y}, \text{succ}_{\text{PB}}, \text{breed}_{\text{adult}}, \text{succ}_{\text{adult}}, \text{emig}, N_{J_0}, N_{J_1}, N_{J_2}, N_{J_3}, N_{\text{Imm}}, N_{\text{PreB1}}, N_{\text{PreB2}}, N_{\text{PreB3}}, N_{\text{BreedOut}}, N_S, N_F, N_{\text{NonB}}, p_C, p_J, p_{\text{ImmPB}}, p_{\text{BreedOut}}, p_{\text{AdultB}}, p_{\text{AdultNonB}})$$

For the CMR component of our IPM, the individual capture histories were modelled using a multi-event framework with a state-space modelling formulation (Kéry & Schaub 2012c a). This allowed for the estimation of age-stage specific survival and productivity rates accounting for age-stage specific probability of detection. In the capture histories, each individual bird was assigned one of the twelve possible states described above, with the state assignment assumed to be exact. The likelihood of the CMR data is hereby denoted as:

$$L_{\text{CMR}}(m \mid \phi_a, \phi_j, \text{recr}_{6-7y}, \text{recr}_{8+y}, \text{succ}_{\text{PB}}, \text{breed}_{\text{adult}}, \text{succ}_{\text{adult}}, \text{emig}, p_C, p_J, p_{\text{ImmPB}}, p_{\text{BreedOut}}, p_{\text{AdultB}}, p_{\text{AdultNonB}})$$

For the productivity data, we modelled the number of fledglings recorded each year produced by first-time breeders (FTB) and adult birds (AB, i.e. second time breeders or more) using a binomial distribution with probability equal to succ_{PB} and $\text{succ}_{\text{adult}}$ and size equal to the total number of first time and adult breeding pairs, respectively. The likelihood is:

$$L_P(J_0, \text{FTB}, \text{AB} \mid \text{succ}_{\text{PB}}, \text{succ}_{\text{adult}}).$$

Assuming independence between each dataset, the joint IPM likelihood is the product between each component likelihood:

$$L_{IPM}(y, m, Jo, FTB, AB \mid \phi_a, \phi_j, \text{recr}_{6-7y}, \text{recr}_{8+y}, \text{succ}_{PB}, \text{breed}_{adult}, \text{succ}_{adult}, \text{emig}, N_{Jo}, N_{J1}, N_{J2}, N_{J3}, N_{Imm}, N_{PreB1}, N_{PreB2}, N_{PreB3}, N_{BreedOut}, N_S, N_F, N_{NonB}, \rho_C, \rho_J, \rho_{ImmPB}, \rho_{BreedOut}, \rho_{AdultB}, \rho_{AdultNonB}).$$

We specified vague priors for all recapture, survival and breeding parameters, using uniform distributions bounded between 0 and 1: parameter $\sim U(0,1)$. The only exception was the prior for ρ_j , which was instead a uniform distribution bounded between 0 and 0.1:

$\rho_j \sim U(0, 0.1)$. The priors for all age-stages population sizes were set as Poisson distribution with mean $\lambda = 100$, with the exception of the prior of N_{Jo} , which was set as $\lambda = 70$.

Analysis of temporal variability

We modelled the temporal variability of productivity (breed_{adult} and succ_{adult}) and survival (ϕ_a) by including each breeding season (i.e. each recapture occasion) as a temporal random effect. Because of the complex formulation and the large number of parameters in the IPM, the inclusion of temporal random effects on both survival and productivity parameters (which are multiplied by each other to define the transition probabilities) resulted in lack of model convergence. Therefore, we separately included temporal random effects on breed_{adult} , succ_{adult} and ϕ_a in three different IPMs. The inclusion of the random effect in the model was specified using the formula:

$$\text{logit}(\text{breed}_{adult,t}) = \zeta + \varepsilon_{\text{breed},t} \quad \varepsilon_{\text{breed},t} \sim N(0, \sigma^2_{\text{breed}})$$

$$\text{logit}(\text{succ}_{adult,t}) = \eta + \varepsilon_{\text{succ},t} \quad \varepsilon_{\text{succ},t} \sim N(0, \sigma^2_{\text{succ}})$$

$$\text{logit}(\phi_{a,t}) = \theta + \varepsilon_{\phi_a,t} \quad \varepsilon_{\phi_a,t} \sim N(0, \sigma^2_{\phi_a})$$

where ζ , η , θ are the overall mean probabilities of breeding, success and adult survival (on the logit scale); $\varepsilon_{\text{breed},t}$, $\varepsilon_{\text{succ},t}$, $\varepsilon_{\phi_a,t}$ are the temporal random effects, drawn from a Normal distribution with temporal variance (on the logit scale) equal to σ^2_{breed} , σ^2_{succ} , $\sigma^2_{\phi_a}$, respectively. The prior distributions for σ^2_{breed} , σ^2_{succ} and $\sigma^2_{\phi_a}$ were set as uniform distributions bounded between 0 and 2.

Effect of candidate covariates

Due to the IPMs complexity and the impossibility to test for the effect of every variable on each parameter, we adopted the following protocol. Starting from the baseline model formulation (i.e. without random effects), we created a set of IPMs including either local oceanographic variables or large-scale climatic indices. Prior to modelling, we ensured that the explanatory variables were not collinear using variance inflation factors (VIFs) from the AED package (Zuur et al. 2009), with a threshold value of 3. All variables were standardised before model fitting. We used univariate logistic regression to separately investigate the effect of the candidate covariates on ϕ_a , breed_{adult} , succ_{adult} as follows:

$$\text{logit}(\phi_{a,t}) = \beta_0 + w_1 * \beta_1 * X_{1,t} + w_2 * \beta_2 * X_{2,t} + \dots$$

$$\text{logit}(\text{breed}_{adult,t}) = \beta_0 + w_1 * \beta_1 * X_{1,t} + w_2 * \beta_2 * X_{2,t} + \dots$$

$$\text{logit}(\text{succ}_{adult,t}) = \beta_0 + w_1 * \beta_1 * X_{1,t} + w_2 * \beta_2 * X_{2,t} + \dots$$

where β_0 is the intercept; β_1 is the slope of variable 1; $X_{1,t}$ is the candidate explanatory variable 1, indexed by timestep; w_1 is a parameter quantifying the inclusion probability of covariate 1, thus representing its importance in the model (O'Hara & Sillanpää 2009).

As we considered lagged climatic indices and we did not know in advance what was the relevant lag for each variable, we created two IPMs separately testing for the effect of each climatic variable, considering all lags. In the end, based on their inclusion probability, all SOI indices were discarded and only SAM with a 12 month temporal lag was selected.

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CHAPTER 3

Spatial and temporal aggregation of albatross chick mortality events in the Falklands suggests a role for an unidentified infectious disease

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ABSTRACT

In the context of environmental change, determining the causes underpinning unusual mortality events of vertebrate species is a crucial conservation goal. This is particularly true for polar and sub-polar colonial seabirds, often immunologically naïve to new and emerging diseases. Here, we investigate the patterns of black-browed albatross (*Thalassarche melanophris*) chick mortality events unrelated to predation recorded between the 2004/05 and 2019/2020 breeding seasons in four colonies across the species range in the Falklands. The prevalence of these mortality events was highly variable across years, causing the death of between 3% and 40% of all chicks in the studied plots. With few exceptions, mortality was patchily distributed. Using clustering methodologies, we identified the spatio-temporal mortality clusters based on the nest locations and chick death date. Using generalised linear models and generalised additive mixed-effects models we found that chicks nearer the first mortality event were predicted to die before those in more distant nests. The probability of death increased with age and was highest for chicks close to nests where a chick had died previously. Our findings, along with the symptoms consistently exhibited by most deceased chicks in the study, strongly suggest the prevalence of a widespread infectious disease, potentially with a common aetiology, both in areas with regular and with very rare human presence. Understanding the causes driving these disease-related mortality events, which seem different from the outbreaks documented in the literature, is a conservation priority for the Falklands black-browed albatross population, which comprises over 70% of the species global population.

Keywords

Albatross, *Thalassarche melanophris*, chick mortality, brooding, cluster analysis, disease

1. INTRODUCTION

Seabirds are top-predators playing a key role in the marine ecosystems worldwide. They are health indicators of their prey populations and of the whole food chain (Cairns 1988, Monaghan 1996), consuming every year an overall biomass of the same order of magnitude of global fisheries (Cury et al. 2011). Of all avian groups, seabirds are among the most threatened, with 31% of all species globally threatened, a further 11% near threatened and 47% of the species showing declining population trends (Dias et al. 2019). Major threats underlying the observed declines are fishery bycatch, invasive alien species, the current and predicted effects of climate change and the outbreaks of infectious diseases (Dias et al. 2019). In fact, due to their colonial and philopatric behavioural traits, seabirds are among the animal groups most susceptible to disease and parasitic infections (Cairns 1992, Uhart et al. 2018).

Albatrosses (family Diomedidae) are one of the most rapidly declining seabird groups. With the exception of the black-browed albatross (*Thalassarche melanophris*, hereafter BBA), all albatross species are currently listed as threatened or near threatened, with ongoing dramatic population declines documented in several populations (Birdlife International 2018a). The BBA is in the category of "Least Concern" as classified by the IUCN (Birdlife International 2018b) due to recent increases in population sizes in the Falkland Islands and in Chile. The Falkland Islands contain most of the world BBA breeding population (over 70%), concentrated in 12 colonies (Wolfaardt 2013). BBA are long-lived and extremely philopatric birds, with pairs nesting in the same area of a

given sub-colony year after year (usually re-occupying the same nest). They lay clutches of one egg per year (in the beginning of October) with the hatching period occurring during the last three weeks of December. The chick is guarded by one parent (brooding period) for 11-33 days (Catry et al. 2010), and then stays alone in the nest until fledging, which occurs at around 116 days of age (Tickell 2000).

During a longitudinal demographic study on BBA taking place on New Island, West Falklands (Catry et al. 2011), the BBA study cohort survival and breeding success were monitored since the research began in 2003/04, and nestling mortality episodes have been noted annually during the brooding period. Besides mortality events associated to predation by Falkland skuas (*Catharacta antarctica antarctica*) or striated caracaras (*Phalacrocorax australis*), across the different years a variable proportion of nestlings were found dead in the nest, in most cases still guarded by one adult. Suggestive anecdotal records during the brooding period were made a few decades before by Tickell and Pinder (1975), which described the events of chick mortality not related to predation as “virus-like infections”, occurring from “time to time” in the BBA colonies in the Falklands. Yet, such events have never been quantitatively described in any detail.

In this research, we investigate the spatial and temporal patterns of mortality not caused by predation in BBA chicks across multiple study seasons and in multiple colonies. In particular, the objectives of this paper are to:

- (1) Describe the variability of BBA nestling mortality events across multiple breeding seasons and in different colonies, and investigate their spatio-temporal patterns.
- (2) Uncover whether these events are clustered in space and time and quantify the main variables determining their occurrence.

2. MATERIALS AND METHODS

2.1 Study area and study species

Fieldwork was conducted mainly at the Settlement rookery (51°43'S, 61°17'W), New Island (fig. 1), where an ongoing longitudinal monitoring programme has been carried out since the Austral summers of 2003/04. In this study, we analyse data from the 2004/05 to 2009/10, 2018/19 and 2019/20 breeding seasons, when the daily monitoring covered the whole duration of brooding. BBA nest colonially both on coastal cliffs and on clearings amongst tussock grass *Poa flabellata*. Approximately 14,500 BBA pairs breed on New Island, of which more than 1,500 nest in the Settlement rookery (Wolfaardt 2013). Complementary work was done at: Steeple Jason (51°19'S, 61°13'W) during the 2011/12 breeding season; Beauchene (52°54'S, 59°10'W) and Bird Island (52°10'S, 60°55'W), during the 2015/16 season (fig. 1). Steeple Jason and Beauchene are the largest BBA colonies in the world, with approximately 200,000 and 140,000 breeding pairs, respectively. All three sites, particularly Beauchene, are uninhabited and experience a very limited anthropogenic disturbance. Beauchene and Bird Island have never had any farming or grazing, or any introduced mammals, with human utilization being restricted to short trips to capture seals and penguins, mostly in the 18th and 19th centuries.

2.2 Breeding success and chick survival

On New Island, we studied three BBA sub-colonies (A, B and C) where all nests are individually marked (148-215 nests altogether annually between 2004/05-2019/20: 34-52 in sub-colony A; 33-

44 in B; and 74-119 in C). Each sub-colony is located ca. 80 m from the other two. The status of the nest contents was verified on a daily basis for all nests from the date of laying, through the hatching period (mid-December) and until the end of the brooding period (January), and then weekly until the end of February. A chick alive by the end of February was considered fledged, as mortality (all factors combined, including predation) after this period is typically very low. Albatross chicks were weighed when 58 and 60 days old (for the analyses we used an estimate of the mass at 59 days old, calculated as the mean value between the 58 and 60 days measurements) in order to produce an indicator of annual food availability (Cairns 1992, Lyons & Roby 2011). On Steeple Jason, Beauchene and Bird Island, linear transects were established crossing breeding colonies, scattered all over the island, and contents of all nests (empty or with a live or dead chick) within ca. 1.5 m from each transect were sequentially noted down. On Steeple Jason, the work took place on the 25th of December 2011 and 2nd of January 2012; on Beauchene on the 5th of January 2016; on Bird Island on the 3rd of January 2016.

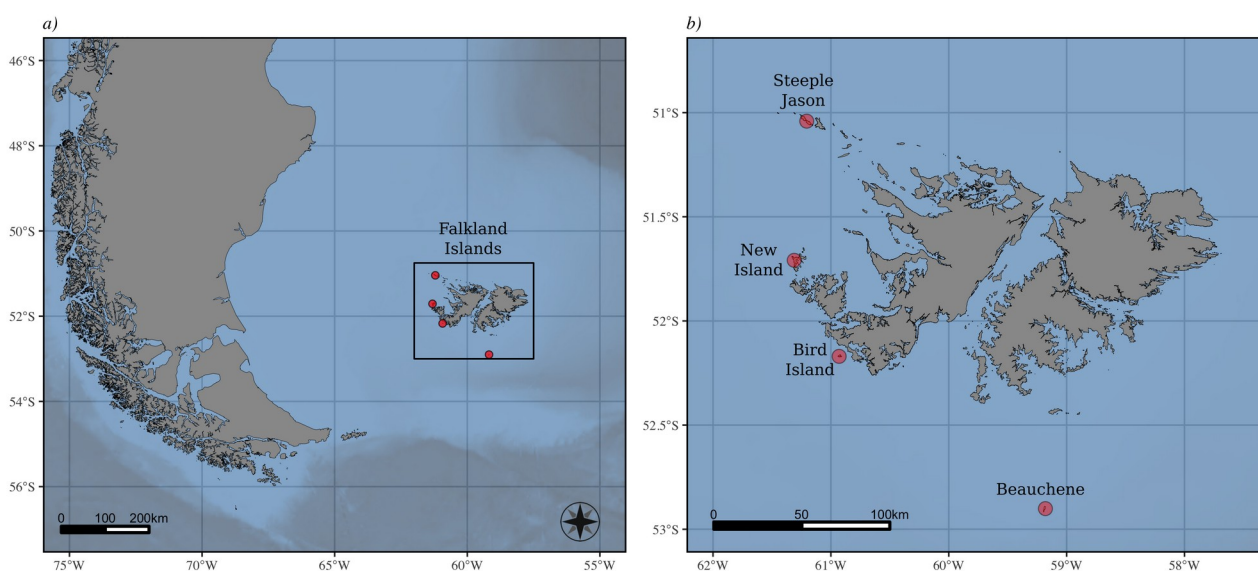


Figure 1 – a) Map of the southwest Atlantic Ocean, with the rectangle indicating the location of the Falkland Islands. b) Finer-scale map showing the locations of our study sites (the colonies of Steeple Jason, New Island, Bird Island and Beauchene, indicated by red dots) in the Falkland Islands.

2.3 Mortality in the nest

We restricted the study of chick mortality to the brooding period because after the chick is left alone for the first time, the causes of mortality are difficult or impossible to determine as predation or scavenging might follow quickly. When daily monitoring the nests, we took note of whether a chick was visibly weak or showed any symptoms of ill-health and, whenever a chick was found dead in the nest, the possible causes were investigated. If a chick was not found in the nest, the mortality was attributed to predation events. While this conservative approach is likely to underestimate the number of chicks dying due to causes other than predation, it ensures that the cases recorded as unrelated to predation were classified correctly.

We used binomial generalised linear models (GLMs) to test whether the variability in the proportion of chicks dead in each sub-colony was captured by the following explanatory variables: sub-colonies, years and the interaction between the two. Using negative binomial GLMs, we investigated whether the variability in age at death was explained by sub-colonies, years and their

interaction. For both modelling approaches, the best models were selected based on AIC (Akaike 1998).

2.4 Spatio-temporal aggregation of mortality

The mortality events taken into consideration in the following analyses are those not caused by predation. To have a minimum number of death cases ensuring statistical power, we carried out fine-scale spatial and spatio-temporal analyses in years where, within a sub-colony, at least 20% of the chicks died of causes other than predation (fig. 2a).

Between the 2003/04 and 2008/09 seasons, all nests of the three sub-colonies studied in New Island were mapped as a lattice by measuring the distance between the centre of each nest and several neighbours (to the nearest 5 cm). All sub-colonies lie in a relatively flat area (albeit slightly inclined) and their overall size is less than 25 m in diameter, so spatial deformations were overall very small. For those seasons, we investigated whether the deaths in our sub-colonies were spatially autocorrelated using Moran's I (Moran 1950), testing the null hypothesis that each case was spatially independent from each other. Moran's I statistical significance (at 0.05 p value) was assessed by a Monte Carlo test using 1000 simulations. On Steeple Jason, Beauchene and Bird Island, we used the Wald-Wolfowitz Runs Test for Randomness to check whether the chicks observed dead in the nests occurred in clusters along the transects.

In order to analyse the spatio-temporal structure of the mortality events, we used cluster and network analysis. Between 2003/04 and 2008/09 (for which explicit spatial data was available), the existence of spatio-temporal clustering was assessed in each sub-colony and year using Gaussian-mixture models (GMMs) and an ad-hoc epidemiological network-based analysis (Cori et al. 2018). To undertake the GMMs clustering, we extracted each observation's spatial coordinates and temporal distance since the first mortality event. We then standardised the variables and clustered the data using GMMs from the `mclust` package (Scrucca et al. 2016) in R (R Core Team 2019). The best model and the optimal number of clusters were chosen based on BIC (Schwarz 1978). The matrices were used to build a spatial and a temporal network, in which the nodes represented the nests and the edges length reflected the spatial and temporal distance, respectively. The networks were then trimmed, disconnecting nodes separated by a spatial (5-m) and temporal (7-days) threshold after which the mortality events were assumed not to be directly connected to each other. Finally, we identified the spatio-temporal mortality clusters by overlapping the trimmed networks and retaining the connections between nodes that were consistent in both graphs. For each cluster identified by each methodology, we calculated the average and maximum spatial and temporal distance between each mortality case and its four closest neighbours in that cluster.

2.5 Effect of spatial and temporal scale and age of chick on mortality

Based on the classification yielded by the previous analytical step, we calculated for each cluster: the temporal lag between each mortality event and the first mortality event in that cluster; and the spatial distance between each nest with mortality and the nest where the first mortality event occurred. Using a negative-binomial GLM, we investigated whether the temporal lag of each case from the first one (i.e. the temporal progression of the mortality events) was explained by the spatial distance between them.

Lastly, we focussed our analysis on the events that occurred in sub-colony C in 2008/09, when approx. 60 % of the chicks died due to causes other than predation. We investigated whether the probability of a chick dying on the nest was affected by the nestling age, by the distance from the

closest chick that died and by the interaction between these two variables. We constructed a dataset in which the status (0 = alive, 1 = dead) of every nest was recorded at every sampling occasion – with the sampling occasions comprising each day that at least one death occurred. For all chicks, at each sampling occasion, we calculated: the age on the specific date; and the distance from the closest nest where a chick died previously. After the chick had died, its status was not recorded in subsequent visits. The constructed dataset was analysed using binomial-based generalised additive mixed models (GAMMs), in which the binary response (alive/dead) was modelled as a function of age (tested both as linear and as smooth term), distance from closest mortality and the interaction between the two. To account for the dependency between observations collected on the same nestling, each chick was included as random effect. All explanatory variables entered the model as cubic regression splines with shrinkage in order to prevent overfitting. The best variables to retain in the GAMM were selected based on AIC.

3. RESULTS

3.1 Mortality in the nest

Across all breeding seasons, in all BBA colonies in this study, most chicks that were found dead in the nest (many still guarded by one adult) consistently showed the following symptoms before dying: swollen gape flanges, serous conjunctival discharge, swollen and purplish coloured inter-phalangeal joints and a lower carriage of the neck, with apparent difficulty in lifting the head up. Most of them were visibly leaner than other chicks of the same age. These symptoms, which usually resulted in the death of the chick within ca. a week of their appearance, were mostly observed when chicks were one to two weeks old. Although not systematically recorded, we only rarely saw chicks with these clinical signs after the period of brood-guarding, and seldom recorded any mortality.

On New Island, mortality events of BBA nestlings not caused by predation showed a high variability across years, both in terms of the numbers of deceased chicks and of the sub-colonies that suffered the highest losses (fig. 2a). Overall, pooling the data from all sub-colonies, the levels of mortality had a variable impact on the breeding success: in different years, from 3.5% up to 40.4% of all chicks died during brooding due to causes unrelated to predation. In seven instances distributed across six breeding seasons (sub-colony A: 2008/09; sub-colony B: 2004/05, 2005/06, 2006/07, 2018/19, 2019/20; sub-colony C: 2008/09), at least 20% of all hatched chicks died due to causes other than predation. In 2008/09, as much as 69 of the 81 (i.e. 85%) deceased chicks in all colonies were not killed by predators (fig. 2a).

The binomial GLM comprising the interaction between year and sub-colony was selected based on AIC, indicating that the mortality levels in different sub-colonies varied across different years (clearly seen in fig. 2a). No significant relationship was found between the annual prevalence of mortality during brooding and apparent annual availability of food, indicated by the mean mass of the chicks at 59 days of age (Pearson's correlation, $r_5 = -0.074$, $p = 0.94$).

The mean age at death (all years and sub-colonies combined) was 10.3 days \pm 5.5 ($n = 170$). The variability in the age of the chicks found dead in the nest (fig. 2b) was explained by the interaction between sub-colony and year in the negative binomial GLM selected based on AIC, suggesting that the age at death varied in different sub-colonies across the different study seasons.

The numbers of dead chicks observed along the transects on Steeple Jason, Beauchene and Bird Island are considerable underestimates of chick mortality, as many dead chicks would have disappeared within a few days of dying. The transects carried out on Steeple Jason during the 2011/12 season revealed that, overall, 12.5% of all chicks seen were dead ($n = 4,554$ nests with chicks, alive or dead) and that 61.9% of all nests ($n = 6,441$) contained a live chick. The transects carried out on Beauchene and Bird Island during the 2015/16 breeding season showed that 2.8 % ($n = 605$ nests with chicks, alive or dead) and 3.2 % ($n = 314$) chicks were dead, respectively. In total, 68.4 % ($n = 860$) and 53.7 % ($n = 566$) of all nests had a live chick in Beauchene and Bird Island, respectively.

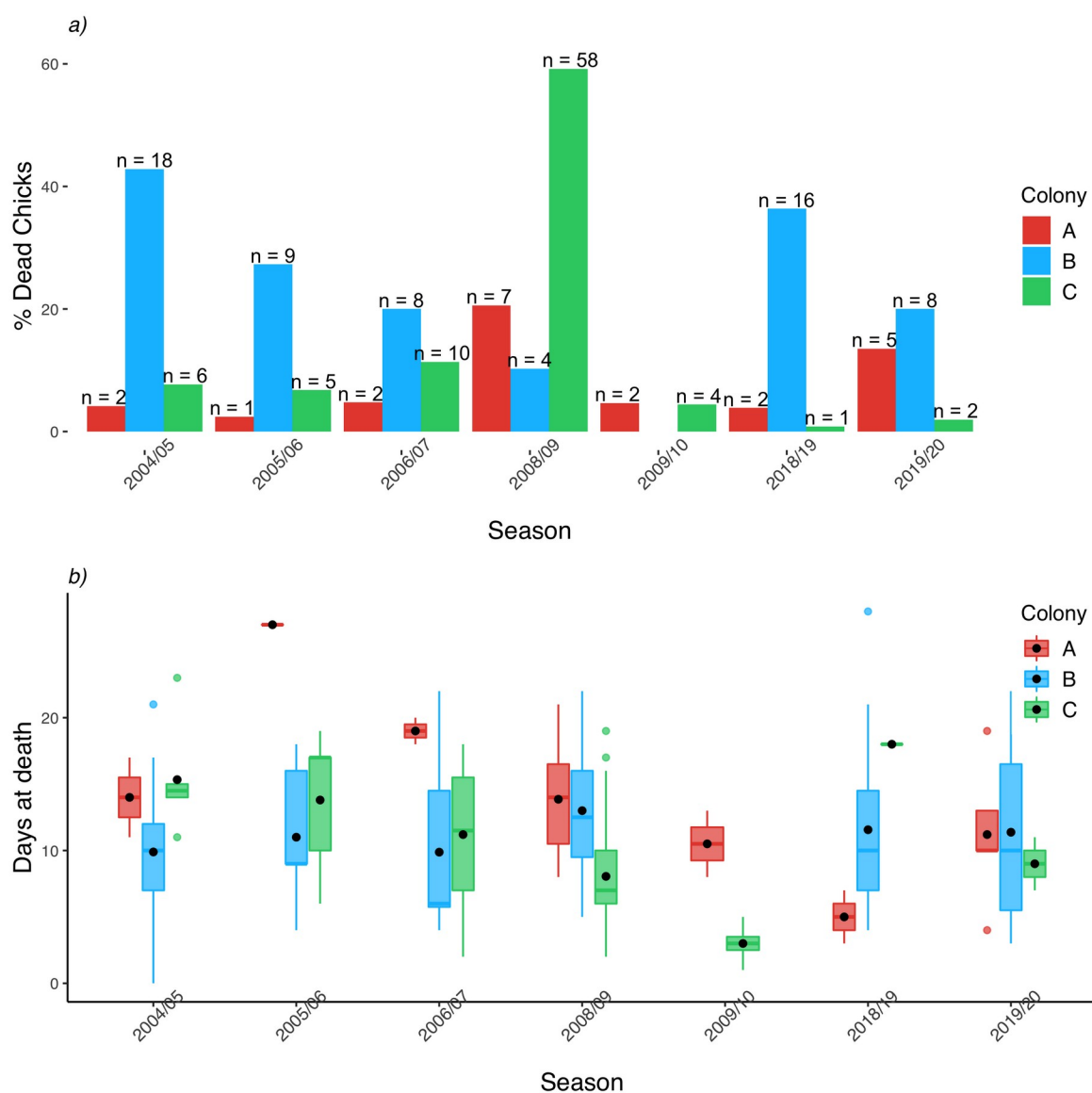


Figure 2 – a) For each year and each sub-colony, the barplot shows the percentage of chicks that died due to causes other than predation. On top of each bar, the respective sub-colony sample size is specified. b) Boxplot showing the age (days) at death (median, 0.25 and 0.75 quantile) in each sub-colony, over the study seasons. The black circle represents the mean and the vertical "whisker" line the range.

3.2 Spatio-temporal aggregation of mortality

The calculated Moran's I indicated spatial clustering of mortality in 2008/09 within sub-colony A (Moran's I = 0.37, $p = 0.001$) and in sub-colony C (Moran's I = 0.17, $p = 0.001$), while near-significant

clustering was found in 2006/07 in sub-colony B (Moran's $I = 0.10$, $p = 0.066$). We found no clustered pattern in the two other situations, both in (the much smaller) sub-colony B (in 2004/05: Moran's $I = -0.06$, $p = 0.594$; in 2005/06: Moran's $I = -0.08$, $p = 0.605$), likely due to small sample sizes.

The results from the Wald-Wolfowitz Runs Test for Randomness for both Steeple Jason (both months) and Beauchene showed that nests with dead chicks were spatially aggregated ($p < 0.0001$ on both occasions) but not on Bird Island ($p = 0.657$). The distribution of nests with live chicks was also aggregated (Steeple Jason, $p < 0.0001$; Beauchene, $p < 0.001$; Bird Island, $p < 0.0001$).

The selected GMMs-based and network-based clusters were identified (fig. 3a). The average and maximum spatial and temporal distance from closest neighbours produced consistent estimates under the two different methodologies (fig. 3b). For the GMMs-based clusters, they were equal to 2.6-3.3 m (average-maximum estimates, respectively) and 4.0-6.5 days, whereas for the network-based clusters, they were equal to 2.4-3.1 m and 5.0-8.4 days.

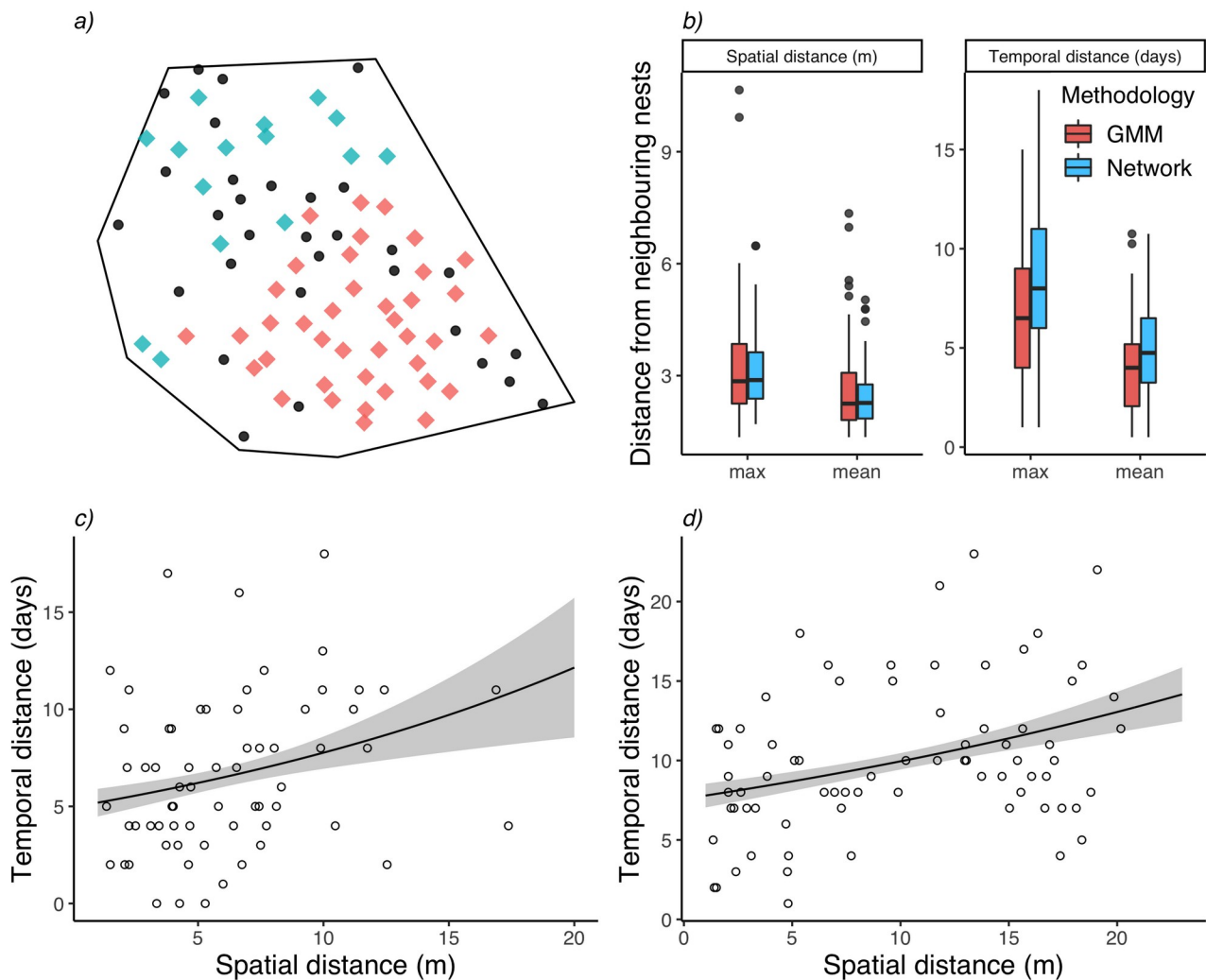


Figure 3 – a) Example of cluster analysis based on Gaussian-mixture models (GMM) for sub-colony C in 2008/2009. The circles represent nests with chicks surviving to fledging or that died due to predation; the rhombuses depict nests that experienced mortality events not caused by predation, with different colours

representing different clusters. b) The average and maximum spatial and temporal distance between each nest in that cluster and its four closest neighbours, calculated for both GMM and network-based clusters. c) and d) Results of the negative binomial generalised linear model based on the output from GMM-based and network-based clusters, respectively. On the y-axis, the temporal lag between each mortality event and the first mortality event in that cluster; on the x-axis, the spatial distance between each nest with mortality and the nest where the first mortality event occurred. The shaded areas represent the 95% confidence intervals and the points are the observed data.

3.3 Effect of spatial and temporal scale and age of chick on mortality

In each cluster, regardless of the methodology used for the cluster classification, the spatial distance between each nest and the nest where the first chick died was retained as a significant explanatory variable determining the temporal progression of the mortality events (GMM-based: $z\text{-value} = 2.124$, $df = 1$, $p = 0.037$; network-based: $z\text{-value} = 3.156$, $df = 1$, $p = 0.002$). In the GMM-based (fig. 3c) and network-based classification (fig. 3d), nests more distant from the mortality starting point took longer to experience mortality events than nests closer to the starting point. More specifically, chicks in nests located 10 m away from the mortality starting point were predicted to die ~ 2.6 and 2.2 days later than chicks that were just 1 m away, respectively.

In the largest mortality instance recorded in our study (sub-colony C, 2008/09 breeding season), both chick age (as linear term) and distance from closest mortality event (as smooth term), but not their interaction, were retained as significant explanatory variables affecting the probability of a chick dying. The probability of dying increased as chicks became older and was highest for chicks in close proximity to a nest where a chick had already died (fig. 4).

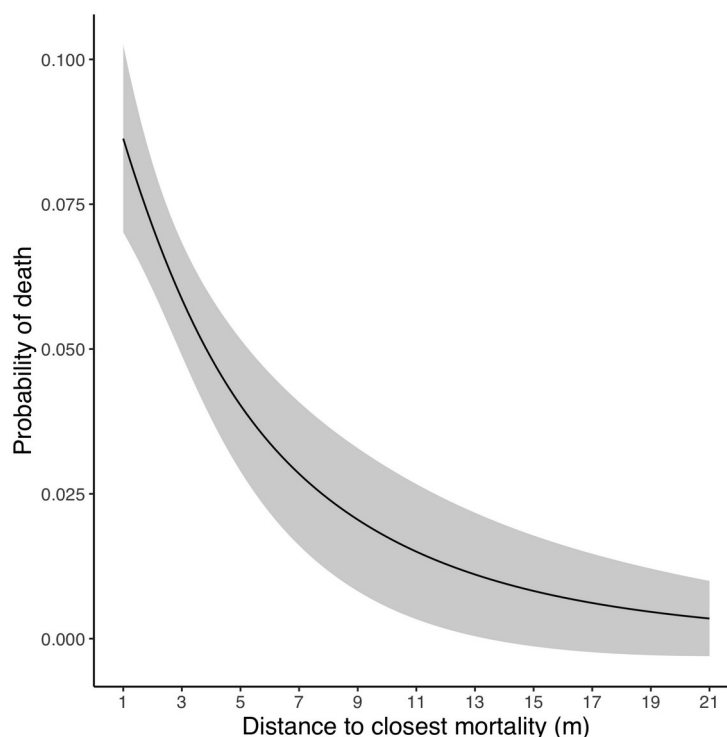


Figure 4 – Results of the generalised additive mixed model (GAMM) for sub-colony C in 2008/09, showing how the probability of death for a 7-day old chick (i.e. the median age at death in sub-colony C in 2008/09, chosen for visualisation purposes) is affected by distance from the closest chick mortality event. The shaded areas are the 95% confidence intervals.

4. DISCUSSION

4.1 Variability of nestling mortality

Between the 2003/04 and 2019/20 breeding seasons, we found variable levels of BBA chick mortality during brooding. In the study plots on New Island, these mortality events decreased the overall breeding success by a minimum of 3.5% and a maximum of over 40%, affecting different sub-colonies to a variable extent in different years. On Steeple Jason, Beauchene and Bird Island, a minimum of 2.8% to a maximum of 12.5% of chicks were found dead in the nest on a single visit (which must be a considerable underestimate of the real number of deaths, see Results above). The prevalence of mortality across years did not correlate with mean chick body mass at 59 days of age, suggesting that the variability in the mortality levels was not explained by malnutrition and insufficient food. Additionally, the results on clustered mortality patterns do not fit within malnutrition as a primary cause of death, as in that case we would expect dead chicks to be evenly distributed throughout the breeding colonies.

4.2 Spatio-temporal aggregation of mortality

On all islands, our results provide evidence of spatial aggregation of mortality. The lack of structuring detected on New Island in sub-colony B might be due to the small area of the sub-colony (ca. 150 m², i.e. ~80% and ~40% of the area of sub-colony A and C, respectively) and to small sample sizes. On Bird Island, while no spatial clustering was detected for the chicks found dead on the nest, there was strong evidence of clustering of live chicks, meaning that the nests not inhabited by live chicks (comprising both dead chicks and empty nests, many of which might have had dead chicks removed) were also clustered. In years when more than 20% of the chicks died for causes unrelated to predation, the finer-scale analysis of the New Islands study plots revealed further insight into the patchy structure of the chick mortality events in space and time. Our results show that, within the identified clusters, the chicks closer to the first mortality event were more likely to die before the nestlings more distant to the mortality starting point. Furthermore, the probability of a chick dying increased as its age also increased, and was highest for chicks occupying nests in proximity of a nest where a chick had died previously.

4.3 The potential role of an unidentified infectious disease

While the identification of the specific agent causing the described mortality was beyond the scope of this paper, our results, providing robust evidence of spatio-temporally clustered mortality patterns, are strongly suggestive of and are consistent with the activity of an infectious disease (Carpenter 2001). Further evidence for the role of an infectious disease is provided by the different susceptibility of chicks of different ages, with chicks being more likely to die as they get older, mostly during their first two weeks of life (mean age at death equal to 10.3 days \pm 5.5 (n = 170)). Given that we mostly detected mortality up to the end of the brooding stage, the spatio-temporal clustering of mortality might have been partly explained by coordination of hatching: however, this was not the case, as we did not detect any significant spatio-temporal clustered patterns –using inhomogeneous space-time K functions (Gabriel & Diggle 2009; result not shown in the text). Together with the spatio-temporal patterns of mortality, the prevalence of an infectious disease with a potentially common aetiology is further suggested by the common symptomatology (described above) exhibited on the days prior to death by a large proportion of chicks.

Previous research has shown that individual seabirds of different quality (with differential foraging ability or capacity of provisioning) may distribute differentially within breeding colonies (Coulson 1968), with higher quality birds occupying the best areas, which might ultimately result into aggregated patterns of chick mortality. However, this does not seem to hold true in our case for the following reasons. Firstly, there is no evidence that albatross colonies are spatially structured on the basis of quality factors, such as age or breeding experience. Secondly, the variable prevalence of mortality in different sub-colonies from one year to the next strongly argues against the possibility that the observed patterns might arise due to the conditions of the colony, or of the birds that inhabit them. In fact, the higher or lower quality of some nesting areas within the colonies, i.e. some sites might be more exposed to physical agents such as wind (which, in any case, should not constitute an issue during brooding given the buffering effect of the parent), cannot explain the variability in mortality prevalence in the same sub-colonies in different years. Additionally, in the vast majority of cases, albatrosses' extreme nest fidelity and high adult survival rates means that the contrasting mortality patterns were recorded even if it was mostly the same birds nesting in the same sub-colonies. Thirdly, as egg laying date and individual quality are not related in albatrosses (Catry et al. 2010), a hypothetical structuring of the colonies based on the birds' quality could only explain the spatial, but not the temporal synchrony of the mortality events.

Seabirds – albatrosses and penguins in particular – are particularly affected by recurrent disease outbreaks (Weimerskirch 2004, Dias et al. 2019), with high population level impacts (Bourret et al. 2018, Uhart et al. 2018). Some of the life history traits common to many seabird species, such as dense colonial nesting habits, a prolonged breeding period and extreme philopatry, make them potentially very vulnerable to disease threats, allowing pathogens to spread quickly during the breeding season and to persist for prolonged periods. Additionally, due to growing human trade and tourism, the exposure of immunologically naïve seabirds (typically nesting on remote and isolated areas) to new pathogens might be increasing in the short term (Phillips et al. 2016). The variability and the comparatively smaller scale of the mortality events described here, compared for instance to the magnitude of the die-offs caused by avian pox and cholera (Woods et al. 2009), the observed symptomatic history and the vast majority of the cases occurring when the chicks are one to two weeks old, do not seem to match the seabird disease outbreaks described in the literature (Uhart et al. 2018). Yet, the consistent results obtained for New Island, Steeple Jason, Beauchene and Bird Island, with dead chicks showing similar symptoms, together with the possibly related reports from Tickell and Pinder (1975), suggest that the occurrence of these mortality events might be historically widespread in the BBA colonies in the Falklands, both in areas visited by humans and in those that are not, potentially sharing a common aetiology.

Various diseases, disease causing agents and potential reservoirs or vectors have been described for albatrosses. For instance, *Pasteurella multocida*, the bacteria responsible for recurrent avian cholera outbreaks over the past decades (Leotta et al. 2006), was linked to poultry and human dispersion even in remote areas of Antarctica (Woods et al. 2009). During the avian cholera outbreaks on Amsterdam Island affecting the population of Indian yellow-nosed albatrosses (*Thalassarche carteri*), scavenging skuas seemed to play an important role in the dispersal of *P. multocida* between colonies (Gamble et al. 2020). The bacteria *Erysipelothrix rhusiopathiae* causing pathologies in Indian yellow-nosed albatrosses might be naturally present in fish or in introduced pigs (Jaeger et al. 2015, Weimerskirch 2016). In the BBA population in South Georgia, migrating species, scavengers and human visitors or researchers seemed to contribute to the transmission of the bacteria *Salmonella newport* (Palmgren et al. 2000). The DNA of *Borrelia garinii*, responsible

for bacterial infections in BBA, was found in *Ixodes uriae* ticks (Olsén et al. 1995). In fact, tick infestation was found to have direct repercussions on colonial seabirds population dynamics (Boulinier & Danchin 1996), inducing nest or even colony abandonment (Duffy 1983), affecting nestlings' physiological parameters (Ferrer & Morandini 2019) and having high potential for the transmission of pathogens such as the bacteria *Borrelia burdogferi* (Olsén et al. 1993) and viruses such as *Xavivirus*, *Flaviviruses*, *Orbivirus*, *Phlebovirus* or *Nairovirus* (Nuttall 1984, Major et al. 2009). Viral pathogens in shy albatrosses (*Thalassarche cauta*) include avian *Paramyxovirus* and the recently discovered zoonotic Hunter Island Group (HIGV) *Phlebovirus* (Wang et al. 2014), which may be spread by different possible vectors, such as phlebotomine sandflies (*Phlebotomus* spp.), mosquitoes and ticks. The *Avipoxvirus* isolates obtained from BBA in the Falklands (Munro 2007) show phylogenetic proximity with *Poxviridae* viruses found in penguins in Argentina, suggesting a widespread and long-term circulation of these pathogens in the region.

Given the unidentified nature of the potential pathogenic agent involved, it is not possible to exclude the influence of human activity on the mortality events documented in this study. On New Island, sealing, whaling and farming took place in the 18th, 19th and 20th century and currently the island is visited by researchers and tourists. However, on Steeple Jason, Beauchene and Bird Island, the potential influence of humans and anthropogenic disturbance on the BBA colonies is extremely limited. Beauchene and Bird Island, in particular, have never experienced any farming or grazing, and did not suffer from the introduction of any mammal species or any use for tourist purposes; they were the object of brief visits until no later than the first half of the 20th century to hunt penguins and seals, and currently only receive a small number of visits from researchers. Thus, even if historically humans might have been responsible for the introduction of this pathology in the archipelago, its transmission to the remote BBA colonies may have occurred indirectly by way of other vectors.

In conclusion, the cause and means of contagion of this disease-related mortality events remain unknown and further investigations would benefit from the examinations of samples of organs from freshly dead chicks in the field. Moreover, the analysis of antibodies in plasma samples collected from BBA (Gamble et al. 2019) or from the scavenging and predatory skuas (Gamble et al. 2020) might reveal crucial insight into the exposure of the avian community to pathogens. A thorough understanding of the causes underpinning the occurrence and the magnitude of these events is of pivotal importance, particularly so in the Falklands, which host more than 70% of the BBA world population. The prevalence of this unidentified infectious disease is a potentially important factor driving the variability in nestling mortality and, in some seasons, had a substantial impact on the BBA breeding success, being yet another identified threat for this species. As almost all albatross species are currently threatened, and since the prevalence and impact of diseases affecting these birds can be modulated by climate change and by the human-related spread of pathogens, we believe that filling important gaps in the current coverage of epidemiological research and understanding the implications for conservation and management is a pressing conservation priority.

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CHAPTER 4

Environmental variability directly affects the prevalence of divorce in monogamous albatrosses

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ABSTRACT

In many socially monogamous species, divorce is a strategy used to correct for sub-optimal partnerships and is informed by measures of previous breeding performance. The environment affects the productivity and survival of populations, thus indirectly affecting divorce via changes in demographic rates. However, whether environmental fluctuations directly modulate the prevalence of divorce in a population remains poorly understood. Here, using a longitudinal dataset on the long-lived black-browed albatross (*Thalassarche melanophris*) as a model organism, we test the hypothesis that environmental variability directly affects divorce. We found that divorce rate varied across years (1% to 8%). Individuals were more likely to divorce after breeding failures. However, regardless of previous breeding performance, the probability of divorce was directly affected by the environment, increasing in years with warm sea surface temperature anomalies (SSTA). Furthermore, our state-space models show that warm SSTA increased the probability of switching mates in females in successful relationships. For the first time, to our knowledge, we document the disruptive effects of challenging environmental conditions on the breeding processes of a monogamous population, potentially mediated by higher reproductive costs, changes in phenology and physiological stress. Environmentally driven divorce may therefore represent an overlooked consequence of global change.

Keywords

divorce, social monogamy, environment, state-space model, seabird, albatross

1. INTRODUCTION

Social monogamy is a widespread mating system, almost ubiquitous in birds, shared by over 90% of avian species (Lack 1968) and also present in some mammal species in the orders Primates, Macroscelidea and Carnivora (Lambert et al. 2018). Different species exhibit various degrees of fidelity to their mate, resulting in different rates of maintenance of pair bonds, which is a function of the rates of widowing but also of divorce (Choudhury 1995, Culina et al. 2015). Owing to intra-sexual competition, the choice of mate is seldom unconstrained and many individuals in the population have to settle with a sub-optimal partnership. Across a wide range of species, divorce was found to be a strategy aimed at correcting for these sub-optimal partnerships, resulting in an improvement of the reproductive success of one or both members of the pair (Blondel et al. 2000, Robert et al. 2014, Culina et al. 2015).

Divorce is often an adaptive behavioural mechanism driven by the 'win–stay, lose–switch' information gathering process, in which measures of previous breeding performance inform the decision of an individual to remate with their old partner (stay) or find a new one (switch) (Choudhury 1995, Bried & Jouventin 2002, Dubois & Cézilly 2002). Several studies on monogamous birds (reviewed in Culina et al. 2015) showed that divorce is triggered by breeding failure and that, in terms of breeding success improvements, females benefitted from divorce more than males (suggesting their role as the 'choosy' sex). The strength of the relationship between failure and divorce and the variability in divorce rates among different species have been widely investigated in light of the species-specific life-history traits, which in turn determine the advantages and disadvantages of mate-change (Choudhury 1995, Bennett & Owens 2002, Jeschke & Kokko 2008). For instance, in long-lived seabirds, the benefits resulting from breeding

with the same partner (improved experience and coordination between the pair members owing to mate familiarity) and the high mate survival probability (which limits the costs of waiting in vain for the reunion with the old partner), as well as the costs involved in attracting and pairing with a new mate, result in low divorce rates (Choudhury 1995, Bried & Jouventin 2002, Bried et al. 2003).

Environmental conditions affect the survival and productivity rates in a population; in turn, this may lead to an indirect link between the environment and divorce, mediated by changes in demographic rates. In addition to that, there is some evidence that environmental conditions and habitat characteristics might play an important direct role in affecting the rate of divorce in a population (Newton & Wyllie 1996, Blondel et al. 2000). Some studies supported the 'habitat-mediated' hypothesis, suggesting that divorce is more common in unstable and lower quality environments (Ens et al. 1996, Blondel et al. 2000, Heg et al. 2003, Culina et al. 2015). However, this hypothesis has seldom been comprehensively tested, and in particular it has only been assessed by focussing on different species or on different populations of the same species in different sites. While this approach might allow for assessing the environmental drivers of divorce in populations facing a wide range of conditions, wild populations in different ecological settings often exhibit substantial ecological differences that might hinder the robustness of a comparative analysis. Conversely, the temporal variability of divorce exhibited by the same population in response to environmental changes has not been investigated. Yet, investigating the temporal variability of divorce rates in a single population monitored across multiple years may provide insights into the role of the environment on the mating strategies of individuals. In fact, in so doing, the role of environmental drivers on divorce can be robustly assessed while accounting for the demographic traits characterizing the study population and the same ecological setting characterizing the study site.

In addition to the habitat-mediated hypothesis, alternative environmental-driven mechanisms were proposed. For instance, previous studies hypothesized that, rather than being driven by the reproductive outcome per se, the decision of retaining or changing mate might be informed by the reproductive outcome relative to the environmental conditions experienced in a given year. Thus, environmental variability may affect the reliability of the 'win-stay, lose-switch' information gathered in previous years, potentially leading to a discounting of the importance of reproductive failures in bad years (Greenfield & Rodriguez 2004, Robert et al. 2014). Moreover, the environment might directly influence the process of sexual selection via 'ecological cross-overs', i.e. through changes in preferences of mate characteristics as the environment changes (Botero & Rubenstein 2012).

In this study, we analyse a long-term demographic dataset of the black-browed albatross (*Thalassarche melanophris*) population in the Falkland Islands. The main objective of this study is to investigate whether, across years, divorce is affected by environmental variability. Owing to the indirect effects of the environment on divorce (mediated by changes in demographic rates, see above), and in order to detect direct environmental effects we adopted an analytical framework to simultaneously investigate the intrinsic (i.e. specific to the pairs, such as the previous reproductive outcome) and extrinsic (i.e. environmental) drivers of divorce. Specifically, we test the following hypotheses.

(Hp 1) Reproductive failure triggers divorce. Moreover, as early failures are potential indicators of mate sterility, incompatibility or poor parental abilities (Culina et al. 2015), we hypothesize that

the timing of the breeding failure modulates the relationship between failure and divorce, with early failures being associated with a higher probability of divorce.

(Hp 2) The prevalence of divorce varies significantly across years as a result of environmental variability. Consistent with the habitat-mediated hypothesis, we hypothesize that divorce rate (at the population level) and the probability of divorce (at the individual level) are higher in lower quality years. In particular, as the productivity of this albatross population was found to be largely affected by sea surface temperature anomalies (hereafter 'SSTA', which was found to decrease the productivity of the population) and by wind intensity (hereafter 'WIND', which had instead a positive effect) (Ventura et al. 2021), we predict that divorce is influenced by changes in SSTA and WIND. Specifically, we expect SSTA to positively affect and WIND to negatively affect the prevalence of divorce.

We carried out an individual-based analysis implementing generalized linear mixed effects models (GLMM) and Bayesian state space models (SSM), in which the intrinsic and extrinsic drivers of divorce were simultaneously assessed. More specifically, using GLMMs, we focussed on the effects of previous breeding performance (accounting for the timing of failure) and environmental variables on the probability of occurrence of a divorce event. Using SSMs, we formulated mate-change (differentiating between divorce and widowhood) as a transition between the different 'states'; in so doing, this framework allowed for decomposing divorce into parameters (and their environmental drivers) determining the transitions between states of the breeding population (Culina et al. 2013).

2. MATERIALS AND METHODS

2.1 The study system and data collected

Since 2003, we have collected capture-mark-recapture data on black-browed albatrosses breeding on New Island, Falklands, home to approximately 15 500 pairs (Catry et al. 2011). Every year, we recorded the encounter histories of every breeding bird nesting in five discrete study sub-colonies on New Island and recorded the identity of the ringed non-breeding birds observed inside or outside of our study patches. Each year, we ringed every new breeder recruiting into the study patches. The fate of each egg and chick was recorded on a daily basis during the incubation (beginning in early October) and brooding phases (starting the second week of December) and on a weekly basis during the post-brooding phase. Starting from the 2008 season, we collected GPS tracking data during incubation and brooding (Catry et al. 2013b), which enabled us to quantify the oceanic areas most intensely used by albatrosses (supplementary material). In a recent study (Ventura et al. 2021), we found that this albatross population is increasing and that the sustained population growth is underpinned by high survival rates of both adults and juveniles and by high productivity rates.

The environmental covariates considered in this study were SSTA and WIND, which affect marine productivity through water mixing and nutrient supply and, in the case of WIND, shape habitat accessibility and transport cost (Barbraud et al. 2012). Importantly, SSTA and WIND were found to greatly impact the breeding parameters of this albatross population (Ventura et al. 2021). Specifically, SSTA was found to have a strong negative effect on the probability of breeding and on breeding success, whereas WIND positively affected breeding success. Monthly multi-scale ultra-high resolution SSTA (expressed in °C) was downloaded from the National Oceanic and Atmospheric Administration at a spatial resolution of 0.01° (<https://coastwatch.pfeg.noaa.gov>).

WIND (ms^{-1}) was calculated from the meridional and zonal components reanalysis downloaded from the European Centre for Medium-Range Weather Forecasts ERA-5 database (<https://cds.climate.copernicus.eu/cdsapp>), at a temporal and spatial resolution of 6 h and 0.25° , respectively. Monthly average WIND rasters were calculated for each month in the study. The relevant spatial extent for the variable extraction was the 90% kernel utilization distribution (Calenge 2019) calculated based on the tracking data (supplementary material). The environmental variables were averaged across a temporal window hypothesized to capture the scale at which the environment acts on mate-choice and divorce. Rather than an instantaneous trigger at a precise moment, we assumed that the decision-making process leading to divorce can happen at various times and may be informed and reinforced over time. We therefore opted for a conservative approach and selected a temporal window large enough to encompass relevant periods from which the decision was informed. This window spanned for a year, from the start of the previous breeding season (in October) to the end of the subsequent non-breeding season (in September) immediately preceding the focal breeding season. Thus, for instance, to investigate the environmental effects on the divorce rate in the 2005 season, we averaged the covariates between October 2004 and September 2005. Prior to the inclusion in the models, the explanatory variables were standardized to facilitate model convergence.

It is important to highlight the resolution mismatch between our detailed individual-based dataset and the yearly environmental covariates, which simultaneously affect all study individuals in a given year. As it is often the case for models deployed on longitudinal data, the analytical depth attained adopting an individual-based framework comes at the cost of exposing the analysis to the issue of pseudoreplication. In our case, this involves the association of the same value of SSTA and WIND to all birds in any given year. However, while we acknowledge that the precision of the parameters of the individual-based models might be misleadingly overestimated, our results are supported by a coarser quasi-binomial generalized linear model (GLM) quantifying the environmental effects on the yearly divorce rate (see below), in which the population-level focus is not affected by pseudoreplication.

2.2 Inter-annual variability and environmental drivers of divorce rate

Consistent with the literature, a divorce event was recorded when at least one member of a breeding pair re-paired with a different mate in the following season, while the prior partner was still alive (Choudhury 1995). We calculated the yearly divorce rate for all study years. We used a quasi-binomial GLM to model the population divorce rate as a function of SSTA and WIND. The significance of each candidate covariates was assessed by fitting nested models in which each explanatory variable was removed in turn and the difference in scaled deviance between the full model and the model without the covariate was compared using a χ^2 test (Zuur et al. 2009).

2.3 Probability of divorce, timing of failure and environmental effects

To investigate the variables affecting the probability of divorce, we considered the encounter histories of all non-widowed females. To restrict our analysis exclusively on the occurrence of divorce events, the females that suffered mate loss were excluded; this resulted in a dataset comprising 2899 breeding attempts recorded for 424 females between the 2004 and the 2019 seasons. Every year, the individuals could either: remain faithful and mate with their previous partner (coded as '0'); skip a breeding attempt while their mate also did not attempt breeding (also coded as '0'); divorce and breed with a new mate (coded as '1'); or skip a breeding attempt while their previous partner bred with another mate (also considered as a divorce and thus coded as '1'). Using binomial GLMMs, we modelled the occurrence of divorce as a function of the

following explanatory variables: the individual previous year breeding score; SSTA and WIND. The individual breeding score (which was preferred to breeding success because it is non-dichotomized, Culina et al. 2015) was calculated as a categorical variable in which successfully fledging a chick was coded as '2'; failed after hatching was coded as '1'; failed before hatching was coded as '0'. Each individual identity was included as a random effect. Starting from a full model with all explanatory variables and interactions, we performed backwards model selection and removed covariates based on Akaike information criteria (Akaike 1998). For completeness, the same analysis was carried out on the encounter histories of males (supplementary material).

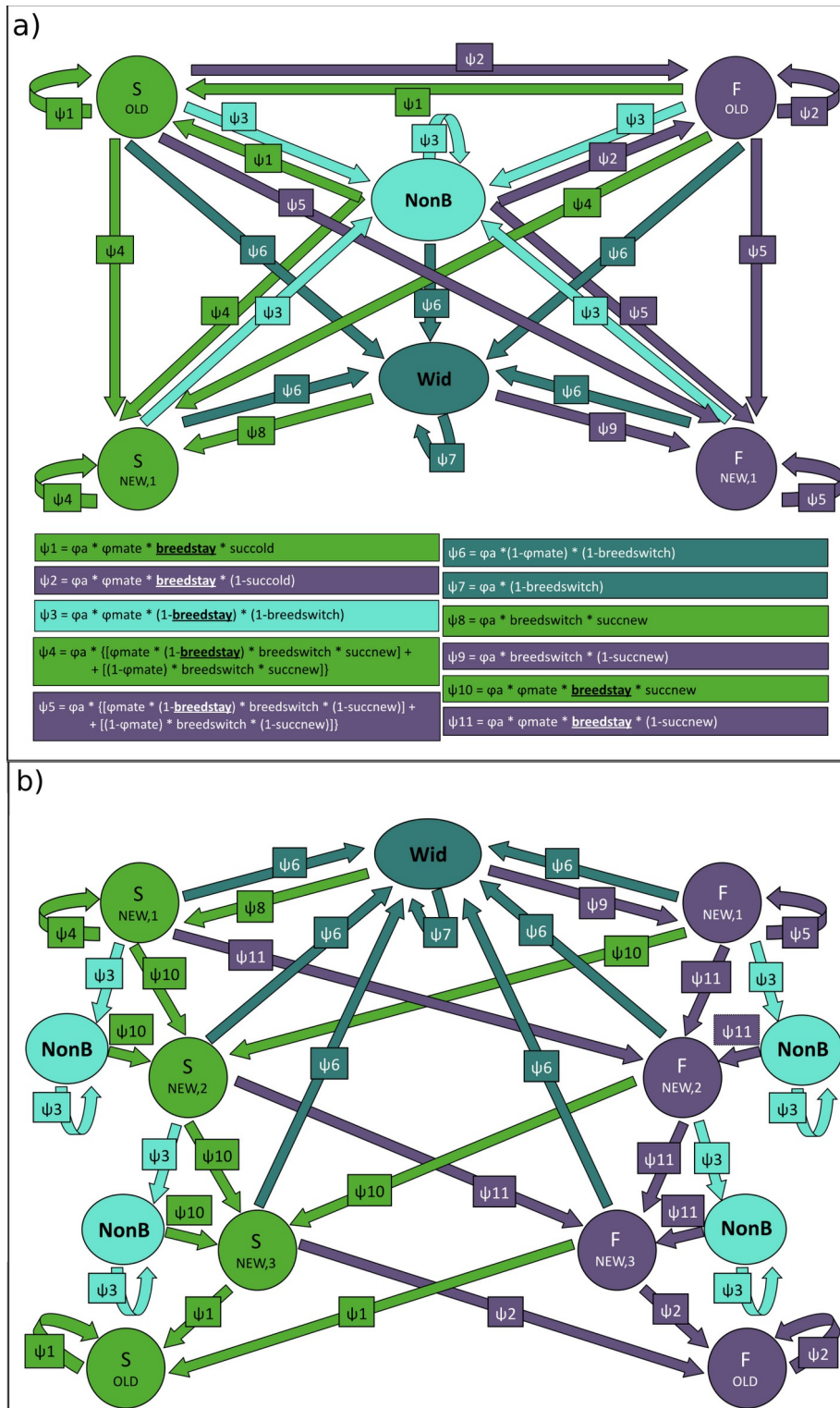


Figure 1 – The multi-event stage-structured Bayesian state-space models (SSM) describing the breeding processes of the black-browed albatross population. Two separate SSMs were set up, one for females and the other for males. The models were applied to all encounter histories of females and males, including those with zero and multiple mate-changes. For clarity, the model diagram is divided in two panels. In (a), we represent the transitions of the 'old' states and the first year 'new' states. In (b), we depict the transitions of the 'new' states, which revert to 'old' after the third breeding attempt (see below and section 2.4 in the main text). The states are: successful (S_{OLD}) or failed (F_{OLD}) birds breeding with the old mate; successful (S_{NEW}) or failed (F_{NEW}) individuals breeding with a new mate, where a relationship is defined as 'new' for the first 3 years (S/F_{NEW1} , S/F_{NEW2} , S/F_{NEW3}), after which the individuals automatically transition to the 'old' states; non-breeding (NonB), if they skipped breeding and their partner was alive; widowed (Wid), if their previous mate died and they did not breed with a new one. In both panels, the same names are used for the same states—i.e. NonB in (b) is the same state as in (a). The different colours are used to represent successful and failed breeders (both with an old and a new mate), non breeders and widowed. The transition probabilities between states (ψ), shown in the equation boxes at the bottom of (a), are driven by state-specific parameters. The complete set of state-specific parameters, determining the transitions between states, were: probability of retaining the previous mate (breed_{STAY}); probability of breeding after mate-change (breed_{SWITCH}); breeding success with the first mate (succ_{OLD}) or with subsequent mates (succ_{NEW}); individual survival (ϕ_a); partner survival (ϕ_{mate}). In the equation boxes, the breed_{STAY} parameters for the different states are represented using bold underlined text to highlight that, within the model formulation, the environmental effects on the state-specific breed_{STAY} parameters were quantified using logistic regression.

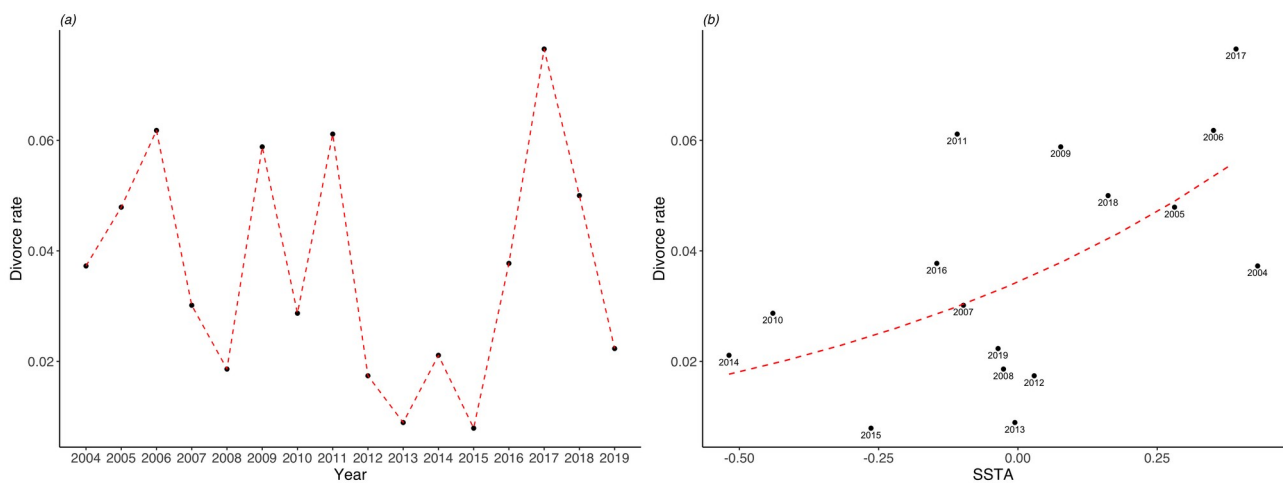


Figure 2 – (a) The temporal variability in divorce rate between 2004 and 2019. A divorce event was recorded when at least one member of a pair re-paired with a different mate in the following season, while the old partner was still alive. (b) The predicted effect of sea surface temperature anomaly (SSTA) on the population divorce rate based on the quasi-binomial GLM, depicted by the dashed red line. The dots represent the observed divorce rate (on the y-axis) and SSTA (on the x-axis), with the labels specifying the year in which each observation was recorded.

2.4 Retaining mate, switching mate and environmental effects

The focus of our analysis then moved from modelling the probability of occurrence of a divorce event (described in section 2.3) to a finer scale, individual based investigation of mate-change (i.e. focussing on both divorce and widowing). Mate-change (owing to divorce or widowing) was formulated as transition determined by two key parameters: the probability of retaining the previous mate; and the probability of breeding after mate-change (i.e. 'switching mate' after divorce or mate loss). The objective of the analysis was to compare these parameters among

previously successful, failed, non-breeding and widowed birds; and to investigate whether changes in environmental covariates affected the probability of retaining the previous mate for the different states of the breeding population. Separately for females and males, we built stage-structured Bayesian SSMs adopting a multi-event framework (figure 1; supplementary material) to quantify the state-specific probabilities of retaining the previous mate ($\text{breed}_{\text{STAY}}$) and of breeding after mate-change ($\text{breed}_{\text{SWITCH}}$). In the models, each individual entered the cohort the year after recruiting (i.e. the year after their first breeding attempt). We specified different $\text{breed}_{\text{STAY}}$ parameters for previously successful (i.e. successfully fledging a chick), failed and non-breeding individuals; and a different $\text{breed}_{\text{SWITCH}}$ for previously successful, failed, non-breeding and widowed birds. In short (see supplementary material for a detailed description), the encounter histories of all females ($n=463$) and males ($n=477$) were retained in the analysis. Every season, the individuals were assigned to one of the following states: successful (S_{OLD}) or failed (F_{OLD}) with the old mate; successful (S_{NEW}) or failed (F_{NEW}) with a new mate; non-breeding (NonB), if they skipped a reproductive attempt and their partner was alive; widowed (Wid), if their previous mate died and they did not breed with a new one. Every time that an individual did not retain the previous mate and bred with a new mate, it transitioned to S_{NEW} or F_{NEW} , depending on the outcome of the reproductive attempt. The individuals automatically transitioned to S_{OLD} or F_{OLD} after the third breeding attempt with the same new mate. When designing this SSM, we made the following two assumptions. First, to decide whether assigning non-nesting individuals to the NonB or Wid state, we assumed that their previous mates were dead if they were not seen during that breeding season and never sighted again. The validity of this assumption is supported by the ecological features of our study population. In fact, the very high detection and survival probabilities of adult birds in our colonies (supplementary material and Ventura et al. 2021) ensure a low probability of misclassifying individuals not seen over a single sampling occasion (i.e. the probability of a bird surviving and of a failed detection), which further drops for individuals not seen over multiple seasons (see supplementary material). Furthermore, it is reasonable to expect that the occurrence of these few (if any) potential instances of erroneous state assignments would not lead to any bias regarding the relationship between the environment and divorce (supplementary material). Second, we assumed that a partnership was 'new' for the first three breeding attempts, after which a mate was considered 'old'. While we acknowledge the subjectivity of this criterion, this decision was taken in order to: capture multiple mate changes; and to improve the biological realism (and therefore the parameter estimates) of the SSM by using different breeding success parameters for new pairs and for well-established, more coordinated pairs (supplementary material).

Within both the female and male SSM formulations, to investigate the environmental drivers of divorce, we used univariate logistic regression to investigate the effects of SSTA and WIND on the probability of retaining the previous mate ($\text{breed}_{\text{STAY}}$). The importance of the covariates was assessed using inclusion probability parameters w (O'Hara & Sillanpää 2009) (supplementary material).

As described above, this SSM was used to analyse the encounter histories of all individuals in our colonies, also including those that never changed mate. This was advantageous for the retrieval of unbiased ' $\text{breed}_{\text{STAY}}$ ' and ' $\text{breed}_{\text{SWITCH}}$ ' parameters. However, the breeding success parameters estimated in this model were not conditional on mate-change having occurred. Moreover, owing to model convergence issues, it was not possible to specify different breeding success parameters for birds that changed mate owing to divorce and owing to widowhood. Therefore, separately for females and males, we designed a second SSM (supplementary material) to quantify the breeding

success before and after mate-change, using different parameters for birds that changed mate owing to divorce and widowhood. To ensure that the estimated breeding success rates were conditional on mate-change having occurred and in order to simplify the model formulation and reach model convergence, we retained in the analysis only those individuals that changed mate once owing to widowhood or divorce.

2.5 State space model implementation

The SSM analysis was performed in the JAGS software executed through R (R Core Team 2019) via the R2JAGS package (Su & Yajima 2012). The Markov chain Monte Carlo algorithm was used to sample from the posterior distribution of each SSM parameter. For all models, we generated three chains of at least 30000 iterations. We ensured that the chains were well mixed and that the Gelman–Rubin diagnostic convergence statistic (Brooks & Gelman 1998) was below 1.02 for all parameters.

3. RESULTS

3.1 Inter-annual variability and environmental drivers of divorce rate

The divorce rate showed a pronounced inter-annual variability (figure 2a): the average rate was 3.7%, ranging between 0.8% and 7.7%. The yearly estimates of divorce rate were significantly positively correlated with SSTA (Pearson's correlation, $r_{14} = 0.57$, $p = 0.02$) but not correlated with the yearly number of available widowed males (Pearson's correlation, $r_{14} = 0.22$, $p = 0.41$) and females (Pearson's correlation, $r_{14} = 0.18$, $p = 0.50$). The divorce rate increased as SSTA increased (figure 2b); SSTA was the only covariate retained in the quasi-binomial GLM ($\chi^2_{1} = 6.8$, $p = 0.009$), explaining 35% of variance in divorce rate ($r^2 = 0.35$).

3.2 Probability of divorce, timing of failure and environmental effects

The GLMM results show that reproductive failure, particularly at an early stage, is the main trigger of divorce. Crucially, after accounting for the effect of breeding failure, our results also show that the probability of divorce increased as SSTA increased. More specifically, the selected GLMMs retained previous breeding score and SSTA (but not their interaction) as significant predictors of the probability of divorce. Previous breeding score was the main variable affecting the probability of divorce—for females whose eggs did not hatch, divorce was approximately: 5.2 times more likely compared to females that failed after their eggs hatched; and 5.4 times more likely compared to successful birds. Additionally, consistently across the different levels of previous breeding score, the probability of occurrence of divorce increased by 1 per cent point (i.e. an increase of 0.18 on the logit scale) for an increase of one standard deviation in SSTA (supplementary material). These results were largely consistent with those obtained from the analysis based on the encounter histories of males (supplementary material).

3.3 Retaining mate, switching mate and environmental effects

The SSM results show that: individuals that failed breeding and those that skipped a breeding attempt were less likely to retain their mate than previously successful birds; and that, after mate change, males were less likely to breed again with a new partner than females. The estimated parameters are represented in figure 3a (for a full description of the model results see supplementary material). In females, the probability of retaining mate (breed_{STAY}) was estimated at 0.97 for previously successful (95% credible interval, hereafter 'CRI': 0.95–0.98); 0.87 for failed

(CRI: 0.85–0.90); and 0.11 for non-breeders (CRI: 0.07–0.16). The male estimates were in line with those for females, with the exception of non-breeding males, for which $\text{breed}_{\text{STAY}}$ was estimated at 0.08 (CRI: 0.05–0.10). In females that did not breed again with their previous mate, the probability of breeding after mate-change ($\text{breed}_{\text{SWITCH}}$) was equal to 0.45 for previously successful (CRI: 0.36–0.55); 0.47 for failed (CRI: 0.39–0.55); 0.59 for non-breeders (CRI: 0.47–0.70); and 0.85 for widowed (CRI: 0.75–0.93). In males, $\text{breed}_{\text{SWITCH}}$ was estimated at 0.26 for previously successful (CRI: 0.20–0.33); 0.26 for failed (CRI: 0.19–0.33); 0.45 for non-breeders (CRI: 0.37–0.53); and 0.65 for widowed (CRI: 0.58–0.72).

The only covariate retained in the SSMs was SSTA for previously successful females (figure 3b): more specifically, the probability of retaining the previous mate ($\text{breed}_{\text{STAY}}$) of previously successful females was negatively affected by SSTA (inclusion probability $w = 0.72$; $\beta_{\text{SSTA}} = -0.39$; CRI: $-8.08, -8.22$).

The results of the SSM formulated to quantify the breeding success before and after mate-change show that the breeding success of females improved after divorce, albeit to a marginal extent. Specifically, the female success before mate change (approx. 0.65) was lower than the breeding success after mate change in case of divorce but higher than the success attained after widowhood (approx. 0.69 and approx. 0.47, respectively, see supplementary material). Conversely, in males, the breeding success estimates were only minimally different before and after mate change (approx. 0.63 before mate change; approx. 0.65 after divorce; approx. 0.66 after widowhood; supplementary material).

4. DISCUSSION

A series of causal and functional explanations of divorce were proposed over the past decades, giving rise to well-established hypotheses in the ecological literature (Choudhury 1995, Culina et al. 2015). As we found that divorce is triggered by breeding failure and that it yields reproductive benefits (particularly so in females, which are more likely to find new partners and attain a higher breeding success), our results strongly highlight that, in a long-lived monogamous seabird population, divorce is an adaptive strategy driven by the 'win–stay, lose–switch' information gathering process. However, crucially, we also found that the divorce rate in our study population varies substantially across years and is directly modulated by temporal environmental variability, with higher divorce rates recorded in lower quality years. To the best of our knowledge, this is the first empirical evidence in support of the habitat-mediated hypothesis tested under a temporal perspective, revealing the effects of temporal environmental variability on the prevalence of divorce in a socially monogamous population. Owing to the particularly advantageous features of our study population (see above and supplementary material), the validity of the assumption of exact state assignment in our multi-event SSM framework is strongly supported. Nevertheless, given its flexibility, the analytical framework developed in this study can be extended to other species by incorporating a probabilistic state assignment formulation to better account for uncertainty in the assignment of widowed and non-breeding individuals. In turn, our methodology promises to be widely applicable to investigate the drivers and the consequences of divorce in other study systems and, more in general, to address ecological questions on the effects of the environment on the breeding processes in a wide range of other socially monogamous species.

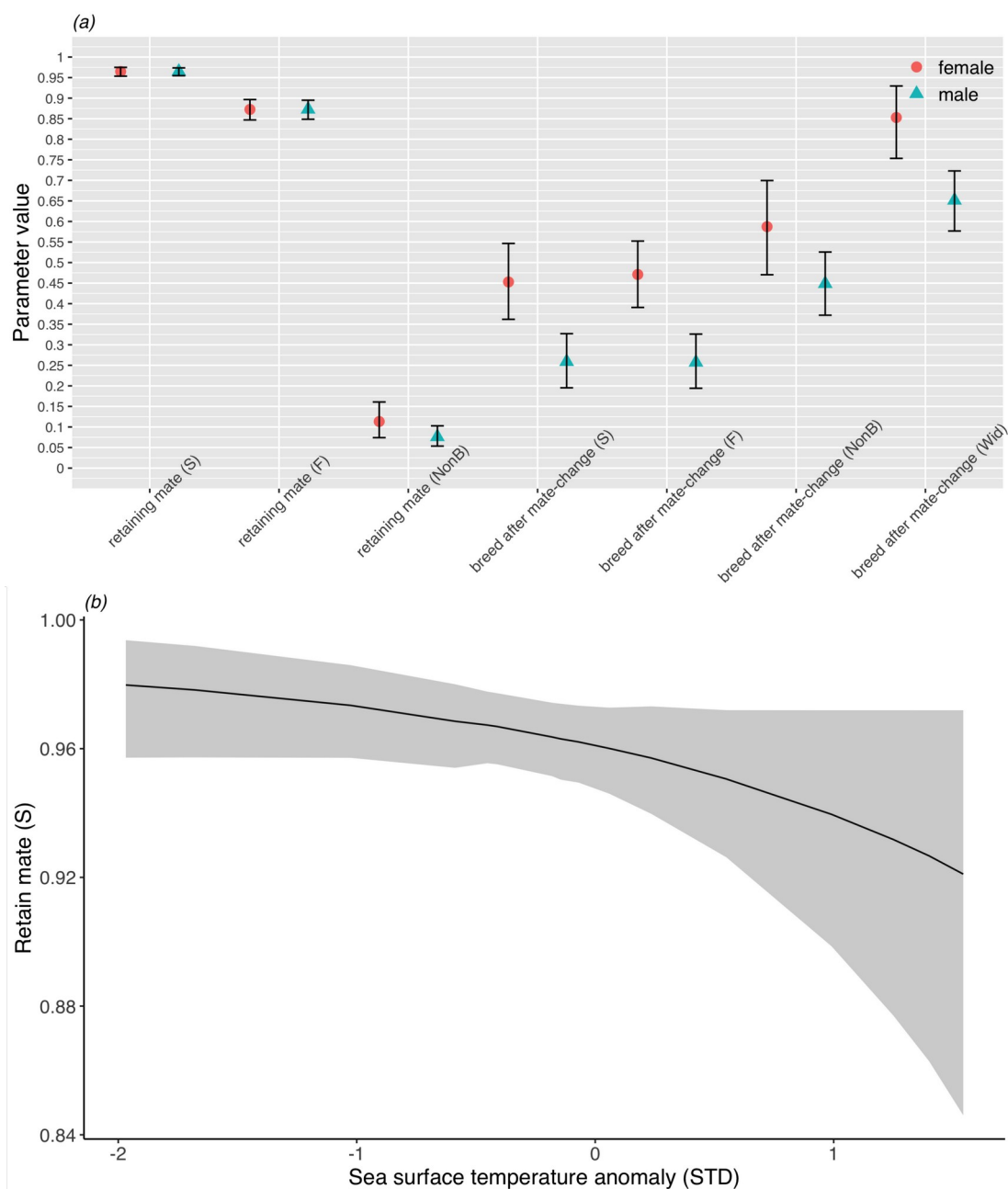


Figure 3 – (a) The probabilities of retaining the previous mate ($\text{breed}_{\text{STAY}}$ in the text) for successful (S), failed (F) and non-breeding (NonB) individuals and the probabilities of breeding after mate-change ($\text{breed}_{\text{SWITCH}}$ in the text) for previously successful (S), failed (F) non-breeding (NonB) and widowed (Wid) birds estimated by the state space model. The parameters for females (dot) and males (triangle) are shown with the respective 95% credible interval, calculated as the 2.5th to the 97.5th quantile of each parameter posterior distributions. (b) The effect of standardized sea surface temperature anomaly on the probability of retaining the previous mate for previously successful females. The shaded area shows the 95% credible interval, ranging from the 2.5th to the 97.5th quantile of the parameter posterior distribution.

4.1 Hp 1: Reproductive failure triggers divorce

In line with the predictions for long-lived species with stable nesting sites (Choudhury 1995, Bried et al. 2003), the Falklands black-browed albatross population showed high levels of mate fidelity and a relatively low average yearly divorce rate (3.7%). Nevertheless, divorces occurred every year and all our models consistently indicated that failed pairs were less likely to remain together than

successful pairs. Moreover, as shown by the GLMM results, the timing of failure is an important element in divorce. In fact, individuals failing during incubation were five times more likely to divorce their partner than those that failed after hatching or that were successful. Early failures may be indicative of an infertile or incompatible mate (Hasson & Stone 2009). Moreover, as the potentially detrimental effects of the environmental stochasticity on breeding processes accumulate and intensify throughout the different phases of the breeding cycle, the mate parental ability is more clearly signalled during the early breeding stages (Lindström 1999).

The SSM results indicate that, after mate-change, the probability of breeding with a new mate is consistently higher in females than in males, for all the states considered. Furthermore, even if to a limited extent, females were more likely to improve their breeding success after divorce (but not after widowhood) compared to males (supplementary material). Collectively, these findings all support the hypothesis that divorce is an active decision initiated by females, the 'choosing' sex in birds (Orlans 1969, Catry et al. 1997, Cézilly et al. 2000, Bried & Jouventin 2002), triggered by breeding failure. This has been suggested in previous studies and classically recognized in the ecological literature, and is consistent with our results on the comparatively higher reproductive benefits in females, both in terms of a higher probability of finding a new mate and a relatively higher improvement in breeding success. The marginally higher survival rate of males compared to females quantified by our SSM (supplementary material) may be indicative of a higher availability of males. Nevertheless, the higher cost of divorce for males (i.e. lower probability of finding new mates, see also paragraph below, and minimal or no improvements in breeding success) and the non-significant correlation found between the yearly number of available widows and the yearly divorce rate suggests that males are likely less prone to initiate divorce than females. Our conclusion on females being the 'choosing' sex should therefore be robust to a potential slight sex bias.

After mate-change, males are less likely to breed with a new partner than females. This is true particularly for divorced males, which are probably poor quality individuals and have a lower probability of breeding with a new mate compared to widowed males (Catry et al. 1997). Conversely, females that did not retain their mate (particularly those in the non-breeding and widowed states) had the highest probability of breeding with a new mate; however, widowed birds pay the forced mate-change costs with a lower reproductive success (supplementary material), probably because they did not actively choose to divorce their partner and therefore do not gain the benefits of choosing a new, better mate (Choudhury 1995).

4.2 Hp 2: Divorce varies in time and is affected by the environment

The albatross population divorce rate showed a marked inter-annual variability. All our models (which focussed both on population-level rates, such the quasi-binomial GLM, and also on individual-level responses, such as the GLMMs and SSMs) were consistent in showing that this variability is directly modulated by changes in the environment. Our findings show that the environment does not exclusively affect divorce through an indirect pathway by shaping the population productivity. Owing to the analytical depth attained by our analysis, the results of the individual based models (which simultaneously assessed the role of intrinsic and environmental covariates) highlighted that the effects of environmental variability on divorce are in fact not limited to an indirect link mediated by changes in demographic rates. In particular, our models showed an increase in divorce (higher divorce rate at the population level, higher probability of divorce and lower probability of retaining the previous mate at the individual level) in years of warm SSTAs. High SSTAs negatively affect marine primary and secondary productivity (Wilson &

Adamec 2002, Behrenfeld et al. 2006, Barbraud et al. 2012), reducing food availability for seabirds via bottom-up processes (Nevoux et al. 2010, Barbraud et al. 2012, Sydeman et al. 2015, Pardo et al. 2017). In the Falklands black-browed albatross population, high SSTA was found to negatively affect breeding rate and breeding success (Ventura et al. 2021).

Our findings strongly support the habitat-mediated hypothesis: presumably harsh conditions linked to high SSTA play a disruptive role in the population breeding processes and lead to a higher divorce rate. As shown by our GLMM, breeding failure, particularly at early stages of the reproductive period, is the main trigger of divorce; however, together with the effects of the previous breeding score, there is a clear and significant effect of SSTA in increasing the probability of divorce. Crucially, when focussing on the probability of retaining the previous mate, the SSM results suggest that, while the effect of SSTA on males and on previously failed and non-breeding females was not conclusive, it is the females in a previously successful relationship that are mostly affected by the environmental harshness. Hence, the emerging interpretation from the evidence obtained is as follows: while breeding failure is the main trigger of divorce for unsuccessful females, the environment acts upon the ones that, based on the 'win-stay, lose-switch' process, should have remained with their previous mate. The alternative hypothesis of an environmental 'discounting' of breeding failures in resource poor years (Robert et al. 2014) is not supported by our results. In fact, the prediction of this hypothesis is that harsh conditions would decrease the probability of divorce for previously failed breeders, whereas there is no predicted effect of the environment on previously successful birds. Instead, the results of our GLMM show a clear, significant increase in the probability of divorce as SSTA increased (supplementary material), affecting breeding females regardless of their previous breeding score (i.e. the interaction term between environmental covariates and previous breeding score was not retained as significant in our GLMM). In this study, we cannot formally investigate the existence of ecological cross-overs (Botero & Rubenstein 2012). However, given the longevity of albatrosses and the benefits arising from long-term relationships, it is reasonable to assume that changes in the sexual selection process would mainly affect the levels of extra-pair mating rather than divorce (Botero & Rubenstein 2012).

Various non-mutually exclusive mechanisms might underpin the environmental effects on divorce. In seabirds, bad conditions determine higher costs of reproduction and higher breeding effort (Weimerskirch et al. 2001), causing individuals to arrive to the following breeding season later (i.e. affecting the phenology) or in a poorer physiological state (Fayet et al. 2016, Gatt et al. 2020). Environmental effects on the breeding phenology of migratory species might cause asynchronous arrivals to the breeding ground between pair members (Cattry et al. 2013a, Pérez et al. 2014), ultimately promoting divorce (Naves et al. 2006). The higher mortality rate caused by environmental harshness can also decrease the costs of mate-change by increasing the availability of alternative mates, i.e. the widowed individuals (Bried et al. 2003); however, in our monitored population, widowed availability did not correlate with divorce rate.

In resource-poor seasons, the deleterious effects of harsh environmental conditions might misinform the decision-making processes of individuals (and in particular of females, the 'choosy' sex), potentially leading them to attribute their poorer state to a poorer performance of their partners. Thus, a potential mechanistic pathway linking environment, mate choice and divorce rate might be underpinned by physiological stress. Stress hormones are key mediators of breeding and sexual selection processes (Husak & Moore 2008). Recent experimental evidence in finches revealed that 'unsatisfied' females in relationships with sub-optimal partners had a level of corticosterone that was three to four times higher than that observed in females paired with

preferred mates (Griffith et al. 2011). Together with this direct response, breeding with sub-optimal mates might increase, in females, the breeding investment and physiological stress levels to compensate for the poor mate performance (Gowaty et al. 2007). Crucially, in seabirds, hard environmental conditions and food shortage are associated with higher levels of circulating stress hormone corticosterone (Kitaysky et al. 2007, 2010). Thus, after a difficult resource-poor breeding season, the greater effort and higher breeding investment can lead stressed females to disrupt the bond with their previous mate and look for a new one, even if previously successful.

5. CONCLUSIONS

Our work provides, to our knowledge, the first evidence of a significant influence of the prevailing environmental conditions on the prevalence of divorce in a long-lived socially monogamous population. This conclusion is probably not only relevant to our study system. We argue that investigating divorce adopting a temporal perspective may provide critical insight into the role of the environment on divorce in other socially monogamous avian and mammalian populations. Focussing our analytical lens both at the population level (yearly divorce rate) and also at the fine scale individual level (probability of divorce and probability of retaining the previous mate), all the modelling techniques adopted consistently indicated that divorce is triggered by breeding failure, but, crucially, that it is also promoted by environmental harshness. The mate familiarity arising from socially monogamous bonds and the improved coordination between the members of a pair is often essential for successfully raising healthy offspring in the variable, dynamic marine environments exploited by seabirds (Bennett & Owens 2002, Reichard & Boesch 2003). Hence, in light of the dramatic extent of the current climatic changes, the environmentally driven disruptions of the breeding processes of socially monogamous populations might represent an overlooked consequence of global change, with repercussions on demography and population dynamics.

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SUPPLEMENTARY MATERIAL

1. Albatross tracking data and estimate of space use

The available GPS tracking data and the methodology implemented to estimate the space use of breeding black-browed albatrosses (*Thalassarche melanophris*) is described in Chapter 2, Supplementary Material Text S1 and Text S2.

2. State space modelling

We formulated two state space models (SSM), which were separately fit to the encounter histories of females and males. In both model formulations, each individual entered the cohort the year after their first breeding attempt. The first SSM (see below) was designed to quantify the state-specific probabilities of retaining the previous mate and breed after mate-change (due to divorce or mate-loss), adopting a formulation accounting for both zero and multiple mate-changes. However, the caveat of the first SSM formulation was that we used a single breeding success parameter for all the individuals breeding with the "old" mates, including both birds that never changed mate and those that did; furthermore, we use a single parameter to quantify the breeding success with the "new" mates, regardless of whether mate change happened due to widowhood or divorce. The first SSM was therefore not designed to quantify the potential improvements in breeding success as a consequence of divorce. Conversely, in the second SSM we used different parameters to properly capture the breeding success pre- or post mate-change, distinguishing between widowhood and divorce. In the model, we only retained the encounter histories of birds that changed mate once: in turn, the parameters capturing the probability of retaining mate are to be interpreted as conditional on mate-change having occurred.

In both SSMs, mate-change (due to divorce or widowhood) is not modelled as a specific state; rather, it is an event determining the transition between "old" and "new" relationships (in the first SSM) and between pre- and post-mate-change states (in the second SSM, see below). To distinguish between non-breeders and widowed birds, the information on the focal individual was matched with the information on the mate current and future state in our database: if its mate was not seen that year and never seen again in the colony, the focal individual entered the widowed "Wid" state; if the mate was seen, either in the current or in future years, the focal individual entered instead the non-breeding "NonB" state. This approach allowed for estimating different stage-specific parameters for birds that changed mate due to widowhood and divorce (e.g. separate probability of finding a new mate and pre- and post- mate-change success for divorced and widowed birds).

In both models, the transitions between states were driven by the parameters described below, in figure 1 in the main text and in figure S1. The parameters specifying the stage-specific probability of detection linked the "true" state process to the observed data. In both models, we used the following parameters:

- Detection probability of adult breeders (p_{AdultB}).
- Detection probability of non-breeding adults ($p_{\text{AdultNonB}}$).

Vague priors were specified for all parameters, using uniform distributions bounded between 0 and 1: parameter $\sim U(0,1)$. The full set of results obtained in the males and females SSMs are

reported in table S1 (for the first SSM formulation) and table S2 and figure S2 (for the second model formulation).

As explained above, the state assignment of non-breeding and widowed birds was informed using the encounter histories (present and future detections) of their mate. An erroneous classification of individuals as widowed may have occurred if their partner was alive and we failed to detect them in the current and future study years. The probability of making such an error is very low and further drops with the number of sampling years, as explained below. Our study population is characterised by high survival (~ 0.95) and high detection probability of adult birds (~ 0.91 , which is the average between breeding and non breeding birds). Thus, we can calculate the probability of misclassification of an individual in a single sampling occasion: in a given year, the probability of a bird surviving and of a failed detection is $0.95 \times (1 - 0.91) = 0.086$. This figure is indicative of the probability of erroneously assuming the death of an individual that was not detected in the last sampling year. However, this probability drops if the individual encounter history comprises more sampling years. For instance, the probability of a bird surviving and not being detected for 2 years in a row is ~ 0.007 , and so on and so forth. Thus, given the particular ecological features of our study system (high degree of philopatry and breeding rate, mostly no gap years between breeding attempts and high propensity of non nesting adult individuals to return to the colonies during the summer months), a failed detection is a strong proxy for death, particularly so if the individuals were not seen over multiple years. While we expect the issue of misclassification to be extremely limited if an individual was not seen over multiple seasons, we acknowledge that the probability of misclassification is higher (albeit still less than 0.09) if a failed detections occurred in the last season. However, this probability is still reasonably low, suggesting that, out of the total number of widowed males and females in the last season (12 and 6 birds, respectively, well within the overall range across the study years), less than 10% may have been misclassified. Hence, rather than removing the last year from the database (which would have greatly reduced our analytical power), we assumed that those birds that were not seen in our colonies and not sighted again were dead, even when the failed detections occurred in the last season. Moreover, when looking at the capture-mark-recapture database, only 15% (14%) of the females (males) that were not seen during one breeding season were sighted again in the colony. Only 2% (1%) of the females (males) that were not seen for more than one year were ever sighted again in the colony.

The results obtained in this study and the relation found between environment and divorce are therefore most likely robust (or minimally biased) by the potential instances of erroneous state assignments. Even in the case of a few instances of erroneous state assignments in our database, it is reasonable to think that these misclassifications would affect the database in a consistent way and it is therefore highly unlikely that the relationship found between the environment and divorce is an artefact of misclassification. As explained above, misclassification should lead to overestimating the number of widowed birds and underestimating the divorce events. For misclassification to affect the relation found between SSTA and divorce, there should be more misclassifications in "good" (i.e. lower SSTA) years. Thus, in "good" years, more birds should be alive and absent from the colony, causing our detection failures. This is very unlikely as it would imply a lower return rate in good years.

2.1 First SSM: retaining mate, switching mate and environmental effects

In the first SSM (visually represented in figure 1 in the main text), we considered all encounter histories in our database, which comprised 409 females and 416 males, between the 2004/05 and the 2019/2020 breeding seasons. The SSM was built as a stage structured SSM with ten stages;

the individual capture histories were modelled using a multi-event framework (Kéry & Schaub 2012a b). This allowed for the estimation of stage specific rates accounting for stage specific probabilities of detection. In the capture histories, each individual bird was assigned one of the ten possible states described below, with the state assignment assumed to be exact:

- successful (S_{OLD}) or failed (F_{OLD}) with the old mate.
- successful (S_{NEW}) or failed (F_{NEW}) with a new mate. To capture multiple mate changes in the encounter histories, a mate was considered "new" for the first three years, in which the focal individual transitioned from S/F_{NEW1} , to S/F_{NEW2} and finally S/F_{NEW3} ; after the third year, it transitioned to S_{OLD} or F_{OLD} . An individual transitioned to S/F_{NEW1} every time that it paired with a new individual (e.g. being S/F_{NEW1} , S/F_{NEW2} or S/F_{NEW3} at year t , it could then become S/F_{NEW1} again at year $t+1$ if it bred with a new mate).
- non-breeding (NonB), if the individual skipped a reproductive attempt whilst the partner was alive.
- widowed (Wid), if the previous mate died and the individual did not breed with a new one.

The following parameters determined the transitions between states:

- probability of breeding with the previous mate ($breed_{STAY}$). To capture the effect of previous breeding performance on $breed_{STAY}$, we used different parameters to quantify the probability of retaining the previous mate for previously successful ($breed_{STAY, S}$), failed ($breed_{STAY, F}$) and non-breeding ($breed_{STAY, NonB}$) birds. The same $breed_{STAY}$ parameter was used for birds breeding with a "new" or an "old" mate; in other words, the probability of retaining the previous mate was quantified irrespective of whether the mate was "old" or "new", but only considering the previous breeding outcome. For instance, $breed_{STAY, S}$ was used to model both the transition from S_{OLD} to S_{OLD} and that from S_{NEW1} to S_{NEW2} .
- probability of "switching", i.e. breeding after mate-change ($breed_{SWITCH}$). We specified different parameters for previously successful ($breed_{SWITCH, S}$), failed ($breed_{SWITCH, F}$), non-breeding ($breed_{SWITCH, NonB}$) and widowed ($breed_{SWITCH, Wid}$) birds.
- breeding success with the old mate ($succ_{OLD}$); this parameter captured the probability of fledging a chick with the "old" mate, i.e. considering both the individual's first mate and the subsequent ones after the third year of relationship.
- breeding success with the new mate ($succ_{NEW}$); this parameter captured the probability of fledging a chick with a "new" mate, i.e. it quantified the breeding success in the first three year of relationship. If an individual changed mate multiple times, the same $succ_{NEW}$ parameter was used.
- adult survival (ϕ_A), either females' or males' survival rate from one breeding season to the next, depending on the sex of the individuals in the SSM.
- partner survival (ϕ_{MATE}), similarly as above, either females' or males' survival, depending on the model.

Within this SSM formulation, both for females and males, we investigated the effects of SSTA and wind on the probability of retaining the previous mate ($breed_{STAY}$). Prior to modelling, the variables were standardised and we ensured that the explanatory variables were not collinear using variance inflation factors (VIFs) from the AED package (Zuur et al. 2009), with a threshold

value of 3. We used univariate logistic regression to quantify the effects of the candidate covariates on $\text{breed}_{\text{STAY}}$ for previously successful ($\text{breed}_{\text{STAY},S}$), failed ($\text{breed}_{\text{STAY},F}$) and non-breeding ($\text{breed}_{\text{STAY},\text{NonB}}$) females as follows:

$$\text{logit}(\text{breed}_{\text{STAY},S}) = \beta_0 + w_{\text{SSTA},S} * \beta_{\text{SSTA},S} * \text{SSTA}_t + w_{\text{wind},S} * \beta_{\text{wind},S} * \text{wind}_t$$

$$\text{logit}(\text{breed}_{\text{STAY},F}) = \beta_0 + w_{\text{SSTA},F} * \beta_{\text{SSTA},F} * \text{SSTA}_t + w_{\text{wind},F} * \beta_{\text{wind},F} * \text{wind}_t$$

$$\text{logit}(\text{breed}_{\text{STAY},\text{NonB}}) = \beta_0 + w_{\text{SSTA},\text{NonB}} * \beta_{\text{SSTA},\text{NonB}} * \text{SSTA}_t + w_{\text{wind},\text{NonB}} * \beta_{\text{wind},\text{NonB}} * \text{wind}_t$$

where β_0 is the intercept; β_{SSTA} is the slope of variable SSTA; SSTA_t is the candidate explanatory variable SSTA, indexed by timestep t ; w_{SSTA} is the parameter quantifying the inclusion probability of SSTA, thus representing its importance in the model (O'Hara & Sillanpää 2009). The same applies to wind.

Table S1 – The parameters estimated by the first male and female SSM. We report the mean parameter estimates, the standard deviation (sd) and the 95% credible interval (CRI), ranging from the 2.5th to the 97.5th quantile of each parameter posterior distribution.

Parameter	Mean (sd)	95% CRI
<i>MALE SSM</i>		
Adult survival (ϕ_A)	0.945 (0.004)	0.937, 0.952
Partner (female) survival (ϕ_{MATE})	0.943 (0.005)	0.934, 0.952
Breed with previous mate, prev. successful ($\text{breed}_{\text{STAY},S}$)	0.965 (0.005)	0.955, 0.974
Breed with previous mate, prev. failed ($\text{breed}_{\text{STAY},F}$)	0.873 (0.012)	0.847, 0.895
Breed with previous mate, prev. non-breeder ($\text{breed}_{\text{STAY},\text{NonB}}$)	0.076 (0.013)	0.053, 0.103
Breed after mate-change, prev. successful ($\text{breed}_{\text{SWITCH},S}$)	0.259 (0.034)	0.195, 0.327
Breed after mate-change, prev. failed ($\text{breed}_{\text{SWITCH},F}$)	0.257 (0.034)	0.194, 0.326
Breed after mate-change, prev. non-breeder ($\text{breed}_{\text{SWITCH},\text{NonB}}$)	0.449 (0.039)	0.372, 0.526
Breed after mate-change, prev. widowed ($\text{breed}_{\text{SWITCH},\text{Wid}}$)	0.651 (0.038)	0.577, 0.723
Breeding success with "old" mate (succ_{OLD})	0.680 (0.010)	0.660, 0.700
Breeding success with "new" mate (succ_{NEW})	0.614 (0.019)	0.576, 0.652
Adult breeder (male) recapture probability (p_{AdultB})	0.999 (0.001)	0.997, 0.999
Adult non breeder (male) recapture probability ($p_{\text{AdultNonB}}$)	0.894 (0.017)	0.859, 0.925
<i>FEMALE SSM</i>		
Adult survival (ϕ_A)	0.930 (0.005)	0.920, 0.939
Partner (male) survival (ϕ_{MATE})	0.962 (0.005)	0.952, 0.970
Breed with previous mate, prev. successful ($\text{breed}_{\text{STAY},S}$)	0.965 (0.006)	0.954, 0.975
Breed with previous mate, prev. failed ($\text{breed}_{\text{STAY},F}$)	0.873 (0.013)	0.847, 0.897
Breed with previous mate, prev. non-breeder ($\text{breed}_{\text{STAY},\text{NonB}}$)	0.113 (0.022)	0.074, 0.161
Breed after mate-change, prev. successful ($\text{breed}_{\text{SWITCH},S}$)	0.453 (0.047)	0.362, 0.547

Breed after mate-change, prev. failed ($\text{breed}_{\text{SWITCH},F}$)	0.471 (0.041)	0.391, 0.552
Breed after mate-change, prev. non-breeder ($\text{breed}_{\text{SWITCH},\text{NonB}}$)	0.587 (0.059)	0.470, 0.700
Breed after mate-change, prev. widowed ($\text{breed}_{\text{SWITCH},\text{Wid}}$)	0.853 (0.045)	0.754, 0.930
Breeding success with "old" mate (succ_{OLD})	0.674 (0.011)	0.653, 0.694
Breeding success with "new" mate (succ_{NEW})	0.625 (0.021)	0.584, 0.664
Adult breeder (female) recapture probability (p_{AdultB})	0.999 (0.001)	0.996, 0.999
Adult non breeder (female) recapture probability ($p_{\text{AdultNonB}}$)	0.730 (0.036)	0.658, 0.798
Covariate retained in the female SSM		
Effect of SSTA on $\text{breed}_{\text{STAY},S}$ ($\beta_{\text{SSTA},S}$), on the <i>logit</i> scale	-0.39 (3.034)	-8.081, 8.224

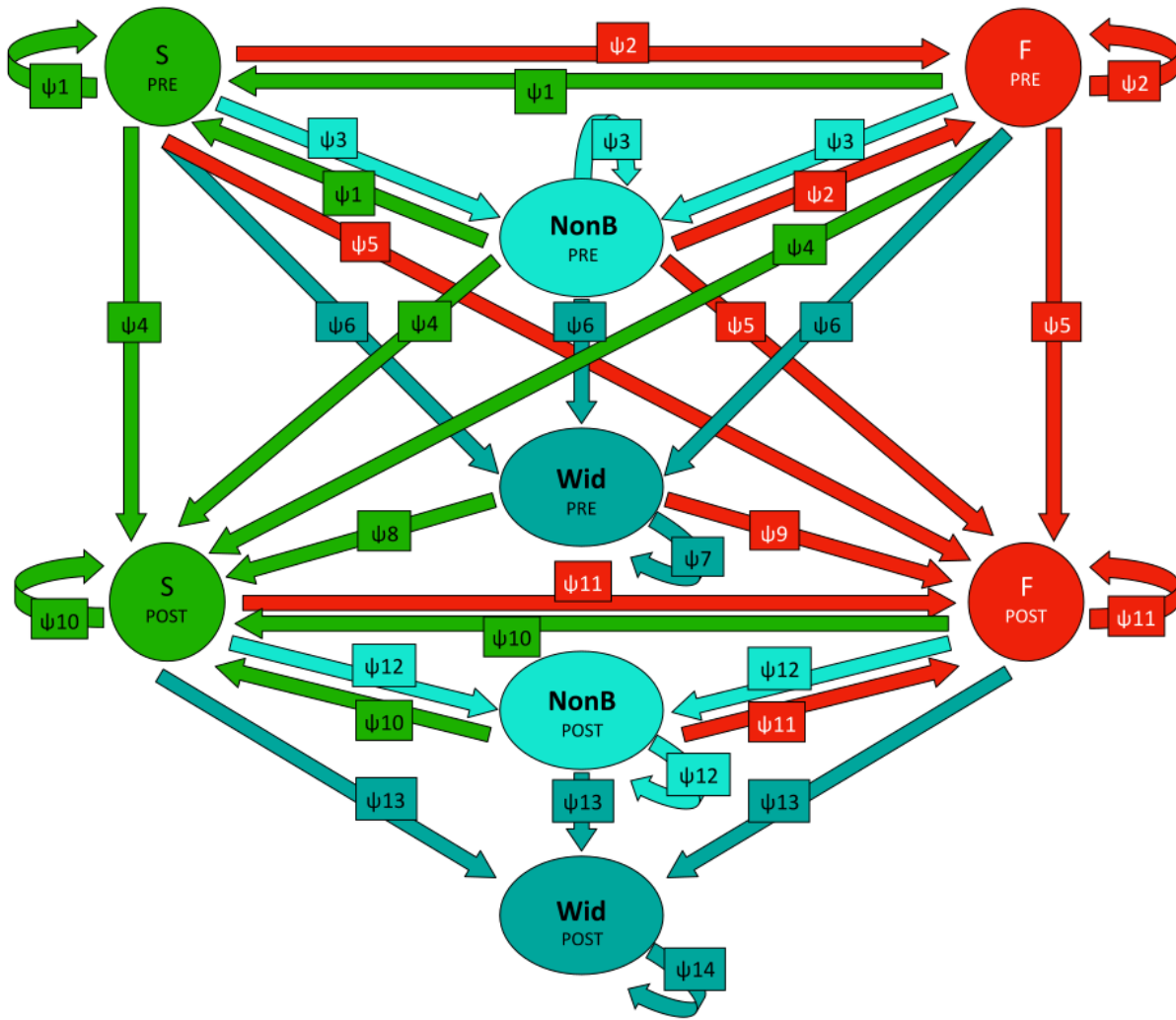
2.2 Second SSM: breeding success pre and post mate-change

In the second SSM (figure S1), we exclusively considered the encounter histories of birds that changed mate only once, resulting in 121 females and 141 males encounter histories, between the 2004/05 and the 2019/2020 breeding seasons. A stage structured SSM with a multi-event framework and the following eight pre- and post mate-change states was built:

- successful (S_{PRE}) or failed (F_{PRE}) with the first mate.
- non-breeding, before mate change (NonB_{PRE}).
- widowed, before mate change (Wid_{PRE}).
- successful (S_{POST}) or failed (F_{POST}) with the second mate.
- non-breeding, after mate change ($\text{NonB}_{\text{POST}}$).
- widowed, after mate change (Wid_{POST}).

The following parameters determined the transition between states in this SSM:

- breeding success with the first mate (succ_{PRE}).
- breeding success with the second mate ($\text{succ}_{\text{POST}}$).
- probability of retaining the first mate ($\text{breed}_{\text{PRE}}$). Different parameters were used to quantify the probability of retaining the first mate for previously successful ($\text{breed}_{\text{PRE},S}$), failed ($\text{breed}_{\text{PRE},F}$) and non-breeding ($\text{breed}_{\text{PRE},\text{NonB}}$) birds.
- probability of "switching", i.e. breeding with the second mate ($\text{breed}_{\text{SWITCH}}$). Different parameters were used for previously successful ($\text{breed}_{\text{SWITCH},S}$), failed ($\text{breed}_{\text{SWITCH},F}$), non-breeding ($\text{breed}_{\text{SWITCH},\text{NonB}}$) and widowed ($\text{breed}_{\text{SWITCH},\text{Wid}}$) birds.
- the probability of retaining the second mate ($\text{breed}_{\text{POST}}$). We specified the same parameters for all birds in the post mate-change states.
- adult survival (ϕ_A), either females' or males' survival rate from one breeding season to the next.
- partner survival (ϕ_{MATE}), similarly as above, either females' or males' survival.



$\psi_1 = \varphi_a * \varphi_{mate} * breed_{pre} * succ_{pre}$	$\psi_8 = \varphi_a * breed_{switch} * succ_{post}$
$\psi_2 = \varphi_a * \varphi_{mate} * breed_{pre} * (1 - succ_{pre})$	$\psi_9 = \varphi_a * breed_{switch} * (1 - succ_{post})$
$\psi_3 = \varphi_a * \varphi_{mate} * (1 - breed_{pre}) * (1 - breed_{switch})$	$\psi_{10} = \varphi_a * \varphi_{mate} * breed_{post} * succ_{post}$
$\psi_4 = \varphi_a * \{[\varphi_{mate} * (1 - breed_{pre}) * breed_{switch} * succ_{post}] + [(1 - \varphi_{mate}) * breed_{switch} * succ_{post}]\}$	$\psi_{11} = \varphi_a * \varphi_{mate} * breed_{post} * (1 - succ_{post})$
$\psi_5 = \varphi_a * \{[\varphi_{mate} * (1 - breed_{pre}) * breed_{switch} * (1 - succ_{post})] + [(1 - \varphi_{mate}) * breed_{switch} * (1 - succ_{post})]\}$	$\psi_{12} = \varphi_a * \varphi_{mate} * (1 - breed_{post})$
$\psi_6 = \varphi_a * (1 - \varphi_{mate}) * (1 - breed_{switch})$	$\psi_{13} = \varphi_a * (1 - \varphi_{mate})$
$\psi_7 = \varphi_a * (1 - breed_{switch})$	$\psi_{14} = \varphi_a$

Figure S1 – The SSM applied to the encounter histories of individuals that changed mate (due to divorce or widow) only once. The state-specific parameters determining the transitions between states, are: the breeding success before ("succ_{PRE}") and after ("succ_{POST}") mate-change; probability of retaining the first mate (breed_{PRE}); the probability of breeding with the new mate (breed_{SWITCH}); the probability of retaining the new (i.e. the second) mate (breed_{POST}); individual survival (φ_a) and mate survival (φ_{mate}). The states are: successful (S), failed (F) non-breeding (NonB) and widowed (Wid), either "pre mate-change" (S/F/NonB/Wid_{PRE}) or "post mate-change" (S/F/NonB/Wid_{POST}).

Table S2 – The parameters estimated by the second male and female SSM. We report the mean parameter estimates, the standard deviation (sd) and the 95% credible interval (CRI), ranging from the 2.5th to the 97.5th quantile of each parameter posterior distribution.

Parameter	Mean (sd)	95% CRI
MALE SSM		
Adult survival (ϕ_A)	0.958 (0.006)	0.945, 0.968
Partner (female) survival (ϕ_{MATE})	0.939 (0.008)	0.922, 0.953
Breed with first mate, prev. successful ($breed_{PRE,S}$)	0.907 (0.018)	0.867, 0.940
Breed with first mate, prev. failed ($breed_{PRE,F}$)	0.790 (0.033)	0.723, 0.850
Breed with first mate, prev. non-breeder ($breed_{PRE,NonB}$)	0.102 (0.036)	0.045, 0.184
Breed with new mate, prev. successful ($breed_{SWITCH,S}$)	0.289 (0.060)	0.182, 0.413
Breed with new mate, prev. failed ($breed_{SWITCH,F}$)	0.346 (0.060)	0.237, 0.470
Breed with new mate, prev. non-breeder ($breed_{SWITCH,NonB}$)	0.555 (0.058)	0.437, 0.665
Breed with new mate, prev. widowed ($breed_{SWITCH,Wid}$)	0.753 (0.049)	0.653, 0.837
Breeding success pre-mate change ($succ_{PRE}$)	0.634 (0.024)	0.586, 0.678
Breeding success post-mate change, divorce ($succ_{POST,Div}$)	0.648 (0.019)	0.610, 0.685
Breeding success post-mate change, widow ($succ_{POST,Wid}$)	0.659 (0.065)	0.531, 0.778
Retain new mate ($breed_{POST}$)	0.939 (0.011)	0.917, 0.958
Adult breeder (male) recapture probability (p_{AdultB})	0.998 (0.002)	0.993, 0.999
Adult non breeder (male) recapture probability ($p_{AdultNonB}$)	0.910 (0.023)	0.858, 0.949
FEMALE SSM		
Adult survival (ϕ_A)	0.949 (0.007)	0.933, 0.962
Partner (male) survival (ϕ_{MATE})	0.970 (0.007)	0.954, 0.983
Breed with first mate, prev. successful ($breed_{PRE,S}$)	0.903 (0.021)	0.860, 0.942
Breed with first mate, prev. failed ($breed_{PRE,F}$)	0.688 (0.037)	0.611, 0.758
Breed with first mate, prev. non-breeder ($breed_{PRE,NonB}$)	0.116 (0.055)	0.033, 0.238
Breed with new mate, prev. successful ($breed_{SWITCH,S}$)	0.614 (0.080)	0.452, 0.758
Breed with new mate, prev. failed ($breed_{SWITCH,F}$)	0.452 (0.061)	0.332, 0.577
Breed with new mate, prev. non-breeder ($breed_{SWITCH,NonB}$)	0.909 (0.050)	0.791, 0.980
Breed with new mate, prev. widowed ($breed_{SWITCH,Wid}$)	0.866 (0.064)	0.721, 0.964
Breeding success pre-mate change ($succ_{PRE}$)	0.648 (0.024)	0.600, 0.696
Breeding success post-mate change, divorce ($succ_{POST,Div}$)	0.693 (0.020)	0.657, 0.732
Breeding success post-mate change, widow ($succ_{POST,Wid}$)	0.468 (0.099)	0.276, 0.658
Retain new mate ($breed_{POST}$)	0.976 (0.007)	0.960, 0.989
Adult breeder (female) recapture probability (p_{AdultB})	0.998 (0.002)	0.993, 0.999
Adult non breeder (female) recapture probability ($p_{AdultNonB}$)	0.807 (0.052)	0.697, 0.903

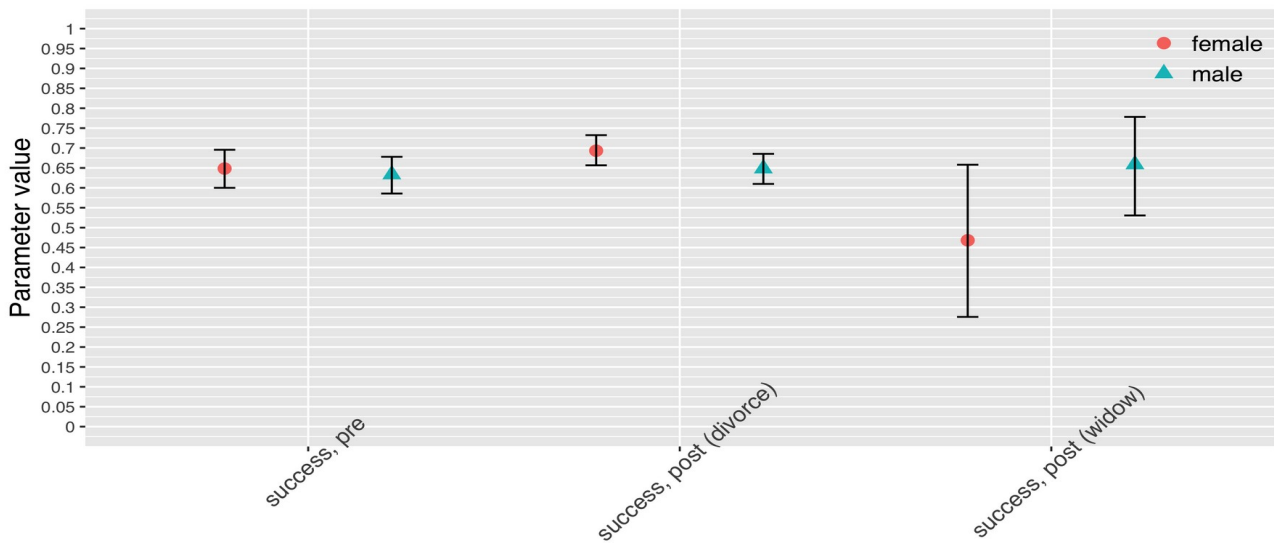


Figure S2 – The breeding success pre- and post mate-change (considering both divorce and widow) yielded by the second SSM, in which only the encounter histories of birds that changed mate once were considered. Dots and triangles are used for females and males, respectively. The parameters are represented with the respective 95% credible interval, calculated as the 2.5th to the 97.5th quantile of each parameter posterior distributions.

3. Generalized linear mixed effects modelling

Binomial generalized linear mixed effects models (GLMMs) were formulated to investigate the probability of occurrence of a divorce event, separately for females (2899 breeding attempts recorded for 424 females between the 2004 and the 2019 seasons) and for males (3095 attempts recorded for 431 males between the 2004 and the 2019 seasons). Only the encounter histories of birds that never changed mate due to widow were retained in the analysis (please refer to the main text and to figure S1 for the distinction between widowed and non-breeding birds).

The individuals in the dataset could either divorce (coded as "1") or not (coded as "0"). Specifically, a divorce event "1" was recorded every time that an individual bred with a new mate while their previous mate was alive; or if a bird skipped a breeding attempt while their previous partner bred with another mate. Conversely, the records in which birds remained faithful and mated with their previous partner or those in which they skipped a breeding attempt while their mate also did not attempt breeding were coded as "0". Separately for females and males, the occurrence of divorce was modelled as a function of: the individual previous year breeding score; SSTA and WIND. The individual breeding score was a categorical variable in which successfully fledging a chick was coded as "2"; failed after hatching was coded as "1"; failed before hatching was coded as "0". Each individual ID was included in the models as a random effect. Backwards model selection was performed based on AIC (please refer to the main text for a more detailed description).

The results obtained in the GLMMs for females and males are largely consistent (figure S3). For both sexes, the probability of occurrence of a divorce event increased with higher SSTA. Specifically, both the selected GLMMs for females and males retained previous breeding score and SSTA (but not their interaction) as significant predictors of the probability of divorce. More specifically, previous breeding score was the main variable affecting the probability of divorce in both sexes. Females that failed before their egg hatched were 5.4 times more likely to divorce

than successful birds and 5.2 times more likely to divorce than females that failed after their egg hatched. Males that failed before their egg hatched were 3.9 times more likely to divorce compared to males that failed after their egg hatched and 4.8 times more likely to divorce than successful males. Moreover, for both females and males, the probability of occurrence of divorce increased as SSTA increased, consistently across the different levels of previous breeding score. In females, an increase of one standard deviation in SSTA led to an increase of 1% (i.e. an increase of 0.18 on the logit scale) in the probability of divorce. In males, an increase of one standard deviation in SSTA resulted in a 1.5% increase (i.e. 0.22 on the logit scale) in the probability of divorce (figure S3).

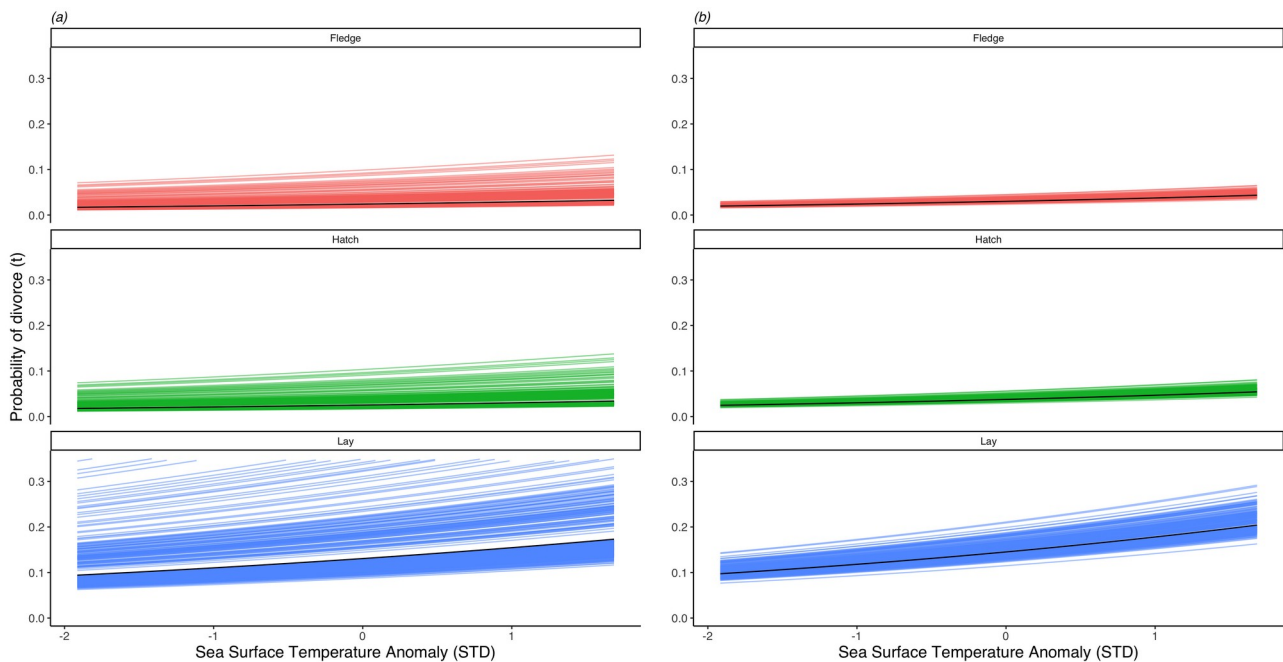


Figure S3 – Results of the GLMM on breeding females (a) and males (b), in which the predicted probability of divorce in season t was modelled as a function of breeding score in year $t-1$ and standardised sea surface temperature anomaly. In both panels, the solid black lines represent the predicted average population responses for the different levels of previous breeding score ("Lay", "Hatch", "Fledge"). The coloured lines in the background show the predicted response of each individual ID.

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CHAPTER 5

Gadfly petrels use knowledge of the windscape, not memorized foraging patches, to optimize foraging trips on ocean-wide scales

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ABSTRACT

Seabirds must often travel vast distances to exploit heterogeneously distributed oceanic resources, but how routes and destinations of foraging trips are optimized remains poorly understood. Among the seabirds, gadfly petrels (*Pterodroma* spp.) are supremely adapted for making efficient use of wind energy in dynamic soaring flight. We used GPS tracking data to investigate the role of wind in the flight behaviour and foraging strategy of the Desertas petrel, *Pterodroma deserta*. We found that rather than visiting foraging hotspots, Desertas petrels maximize prey encounter by covering some of the longest distances known in any animal in a single foraging trip (up to 12 000 km) over deep, pelagic waters. Petrels flew with consistent crosswind (relative wind angle 60°), close to that which maximizes their groundspeed. By combining state–space modelling with a series of comparisons to simulated foraging trips (reshuffled-random, rotated, time-shifted, reversed), we show that this resulted in trajectories that were close to the fastest possible, given the location and time. This wind use is thus consistent both with birds using current winds to fine-tune their routes and, impressively, with an a priori knowledge of predictable regional-scale wind regimes, facilitating efficient flight over great distances before returning to the home colony.

Keywords

flight behaviour, wind, seabird, *Pterodroma*, optimization, state-space model

1. INTRODUCTION

Optimal foraging theory predicts that animals looking for food adopt mechanisms to maximize their energy acquisition per unit time and minimize their energy loss (Tucker 1970, Nathan et al. 2008, Dickinson et al. 2010). The constraints faced by breeding oceanic seabirds — patchily distributed resources and having to return to their colony to alternate incubation shifts with the partner — result in sometimes spectacular foraging trips, many thousands of kilometres from the colony (Rayner et al. 2012, Ramírez et al. 2013, Ramos et al. 2017, Clay et al. 2019). Seabirds thus have morphology and flight behaviour adapted to glean energy for these long commutes from the wind. Nevertheless, how seabirds make use of wind in combination with memory of foraging patches and adaptive search behaviour to maximally exploit oceanic resources remains poorly understood.

Wind fields intrinsically shape the energy expenditure of many seabirds' movements (Weimerskirch et al. 2000, Wakefield et al. 2009, Amelineau et al. 2014), affecting their flight behaviour (Adams & Flora 2010, Gibb et al. 2017) and ultimately, driving changes in population distributions (Suryan et al. 2008) and demographic processes (Weimerskirch et al. 2012, Thorne et al. 2016). Albatrosses, and other procellariiform seabirds, adopt a flight behaviour known as dynamic soaring that exploits vertical wind speed gradients near the sea surface (Pennycuik 2002, Richardson 2011, Sachs et al. 2012). While flying with favourable winds, their energetic consumption is almost as low as when they sit on the nest or rest on the water surface (Weimerskirch et al. 2000, Sakamoto et al. 2013). This, in turn, might constrain the directions that dynamic soaring birds can fly efficiently. Therefore, dynamic soaring *Procellariiformes* must optimize their searching strategies across trade-offs between knowledge about the location and quality of resources and the wind field, which varies to different extents across space and time.

Correspondingly, albatrosses and other seabirds often fly with favourable side and tail winds (Spear & Ainley 1997, Weimerskirch et al. 2000, Wakefield et al. 2009, Paiva et al. 2010) that enable them to travel at high ground speeds and low energetic cost (Weimerskirch et al. 2000, Wakefield et al. 2009, Richardson 2011, Richardson et al. 2018). Their ground speed attained during flight is affected by both relative wind direction (i.e. the difference in angle between wind direction and the bird direction of movement) and relative wind speed or tail wind component, i.e. the wind speed component in direction of the bird's flight (Weimerskirch et al. 2000, Wakefield et al. 2009).

Gadfly petrels (*Pterodroma* spp.) are among the most threatened and least studied seabird genera in the world. As predicted by aerodynamic theory — and as suggested by their genus name (from the Greek words 'Pteron', wing, and 'dromos', run) — the high aspect ratio per wing loading (the highest of all seabirds) makes them especially anatomically adapted for efficient flight: a fast, gliding flight with low profile drag (Spear & Ainley 1997). Gadfly petrels are highly mobile, capable of undertaking exceptionally long foraging trips (Rayner et al. 2012, Ramírez et al. 2013, Ramos et al. 2017, Clay et al. 2019) by spending a large proportion of time in direct flight, actively looking for prey (Rayner et al. 2012, Ramírez et al. 2013). For example, Murphy's petrels (*Pterodroma ultima*) tracked from Henderson Island did not consistently target specific areas and foraged both during directed movement and area restricted search, and the higher mass gains were associated with the most wide-ranging trips (Clay et al. 2019). Despite being the largest genus of pelagic seabirds, with several threatened species, many aspects of gadfly petrels' ecology have never been investigated and, at present, the flight behaviour and the wind use of the long distance flyers par excellence remain largely unknown. Yet, due to their unparalleled motility, these birds could serve as a paradigm to understand the best performing adaptations for efficient flight.

Here we present one of the first GPS tracking datasets available for gadfly petrels, the first on Desertas petrel (*Pterodroma deserta*), collected across three consecutive breeding seasons. Desertas petrel, classified as Vulnerable by the IUCN (Birdlife International 2017), breeds exclusively on the Desertas Islands near Madeira, with an estimated population of ca. 200 pairs. While recent research shed some light on the species' year-round distribution (Ramírez et al. 2013), the processes underpinning their movement ecology during breeding are poorly understood. In this paper, we investigate gadfly petrels' foraging strategy, flight behaviour and use of wind during their long journeys at sea, using Desertas petrels' tracks as a case-study.

In the course of each trip, the birds switch between different movement behavioural modes as their internal motivation changes. For instance, when their motivation is searching for food, they might perform a slower and less direct movement compared with birds transiting between foraging patches. Depending on their motivation, birds are not equally free to optimize their use of wind. These constraints are presumably less pressing during the transit state, when the birds' motivation is to cover distance. Hence, it is when they engage in the transit mode that birds should maximize their flight efficiency and show the most refined behavioural adaptations to efficiently use the wind fields. These predictions should hold true particularly if the birds' foraging strategy does not rely on targeting stable meso- (100–1000 km²) and coarse-scale (1–100 km²) features of the seascape, i.e. if they are unconstrained in their route planning.

A vast body of literature has explored how animals optimize their movement trajectory to maximize prey encounter rate. For instance, it has been proposed that seabirds' search pattern should conform to the Lévy flight foraging hypothesis (Viswanathan et al. 1996, 2008, Humphries et al. 2012; but see Edwards et al. 2007, Palyulin et al. 2014) given the heterogeneous and patchy

nature of the marine resources that they rely upon. In this paper we consider two foraging strategies that can be underpinned by covering long distances at low energetic cost. On the one hand, if the birds target predictably favourable foraging areas, a fast low cost flight allows a higher number of known productive patches to be visited, minimizing the time spent commuting between them. In this case, we expect a significant degree of foraging hotspots overlap across individuals. Further, we expect the return route between the main foraging areas and the colony to be the fastest one, irrespective of the ground covered. On the other hand, if the birds exploit a marine domain with heterogeneous resources distribution and less predictable meso- or coarse-scale features, such as the oceanic waters (Weimerskirch 2007), covering large distances will increase the probability of encountering prey along the route. In this case, we expect a higher flight routes overlap across individuals — particularly if winds are predictable in the area crossed by the birds — but a low overlap in the areas used for foraging by different individuals. Further, we expect that birds choose routes that maximize ground speed, rather than minimizing commuting time between the areas of concentrated searching behaviour and the colony.

Previous studies have shown that travelling seabirds follow prevailing favourable winds (Weimerskirch et al. 2000, Clay et al. 2019), but little is known about the mechanisms with which they manage to do so. Here, we examine whether long distance fliers such as gadfly petrels are capable not only of planning their route based on a priori knowledge of the regional wind regimes, but also of refining their route based on the local wind conditions. If this holds true, we predict that the observed route should be the most favourable one at the specific time and given the local wind conditions experienced by the bird, but it may be a suboptimal solution if it had been carried out at any other time.

Specifically, in this paper we test the following hypotheses:

(Hp1) Birds exploit wind differently during the transit and searching states.

(Hp2) Birds engaging in the transit state use the most favourable relative wind direction, i.e. the one that maximizes their ground speed.

(Hp3) In the pelagic domain used by gadfly petrels, characterized by patchy and unpredictable resources distribution at the coarse- to meso-scale, their foraging strategy relies upon covering large areas at low cost in search of prey along the route, rather than targeting specific foraging grounds.

(Hp4) Petrels optimize their route to cover the largest distance in the shortest time, following predictable regional winds and adjusting their tracks to the local wind conditions experienced en route.

To test Hp1, we use hidden Markov models (HMMs) to classify movement behaviour and compare the birds' wind use during the 'transit' and 'searching' states. To test Hp2, we use generalized additive mixed effects models (hereafter GAMMs) to quantify the effect of wind on the transiting birds' ground speed and to identify the most favourable relative wind direction, which we then compare with the one used most intensively. To address Hp3, we identify and quantify the overlap across individuals in the birds' core searching ('foraging hotspots') and transiting ('travelling hotspots') areas using utilization distributions (UDs), and compare the ground speed and distance covered during the return section of the tracks with simulated 'beeline' homebound tracks; if our hypothesis is true, we expect the travelling hotspots to overlap more than foraging hotspots and the real homebound routes to maximize the ground speed and distance covered. To address Hp4, we adopt a novel spatial and temporal tracks' simulation framework. If petrels both follow

predictable regional winds and adjust tracks to local conditions, we expect the observed routes to be more efficient than the tracks randomized spatially and temporally, respectively.

2. MATERIALS AND METHODS

2.1 The data

We collected GPS tracks at a 2 h temporal resolution on 20 breeding Desertas petrels during three consecutive breeding seasons (2015– 2017). The tracked birds performed both long and short trips. The latter, mostly undertaken after long trips, lasted for an average duration of 28 h, covering the waters in proximity of the colony (average distance from colony = 119 km) and representing only 13.7% of the total time spent at sea by the tracked birds. As we were unsure of the significance of these tracks — possibly not primarily linked to foraging and therefore not representative of the birds' use of wind during foraging trips — we used k-means clustering to categorize trips and only retained long GPS tracks for the analysis (see supplementary material for details). Gaps in the tracking datasets were linearly interpolated using the `adehabitatLT` package (Calenge 2016) in R in order to obtain tracks at 2 h time intervals. The extent of this interpolation was minimal (less than 1% of the points in the final dataset were imputed). We excluded from the analysis the fixes at the beginning or end of each trip falling within a 50 km circular buffer, centred in the colony.

A set of physiographic, oceanographic, biological, distance-related and temporal explanatory variables were extracted for each GPS relocation (supplementary material). They were included in the HMM and tested as explanatory variables for the state-switching probabilities (see below). Fine scale 3 h temporal resolution wind grids were downloaded from the European Centre for Medium-Range Weather Forecasts (<http://apps.ecmwf.int/datasets/data/interim-full-daily/levtype=sfc/>), at a spatial resolution of 0.25° . We extracted wind intensity (expressed in km h^{-1}), wind direction (expressed in degrees), tail wind component (hereafter 'TWC', calculated as in Dell'Ariccia et al. 2018), and wind direction relative to the bird bearing (hereafter ' Δ angle', computed as in Wakefield et al. 2009). As bird bearing and wind direction were expressed using the same reference system (relative to the True North), Δ angle was bounded between 0° (tail winds, blowing on the same direction of movements of the bird) and 180° (head winds, blowing in the opposite direction of movement of the bird).

2.2 Spatial analysis

In order to classify the birds' relocations into 'transiting' or 'searching', the tracks were analysed using the HMM framework using the R package `momentuHMM` (McClintock & Michelot 2018). Based on the observed distance travelled (step length) and the change of movement direction (turning angle) between consecutive relocations, the model estimated the step length and turning angle distributions for the two states considered. The behavioural states of each animal along the track were then decoded using the Viterbi algorithm (Zucchini & MacDonald 2009). To enhance the model's biological realism and to avoid potential confounding effects to the final classification output, we made the following considerations. First, that the probability of transitioning between states may be affected by environmental covariates. Second, that seabirds' speed is intrinsically dependent on the TWC, with longer steps occurring with more favourable winds. We accounted for this in an HMM that modelled the effects of the environmental variables to the state-switching probabilities and simultaneously accounted (through a design matrix) for the effect of TWC on the mean parameter of the step length distributions for both states (details

are provided in the supplementary material). Overall, TWC had a marginal effect on the classification: only 6% of the points changed state as a result of the inclusion of wind into the HMM design matrix.

The overlap between individuals' core foraging and travelling hotspots — defined as the 50% contour of the searching and transiting UD_s, respectively — was calculated using Bhattacharyya's affinity index, as in Oppel et al. (Oppel et al. 2018). Moreover, following Ventura et al. (2019), we bootstrapped the sample of individual UD_s to obtain a robust foraging and travelling hotspots map (supplementary material). The UD_s were calculated using the `adehabitatHR` package in R, with a specified smoothing parameter equal to 120 km, i.e. the longest step length recorded in 2h.

2.3 Wind use analysis

We calculated the distribution of Δ angle in the locations classified as transit and searching. GAMMs from the `mgcv` package (Wood 2006) in R were used to investigate whether Δ angle had an effect on the transiting birds' step length (i.e. their ground speed) and whether this effect is consistent across different values of wind intensity. To do that, the following gamma-based GAMM (hereafter 'wind model') was fitted to the transit section of the tracks:

step length $\sim f(\Delta$ angle) + $f(\text{wind intensity})$, $\text{corAR}_1(\text{Timestep} \mid \text{ID})$,

where the functions f are cubic regression splines with shrinkage, adopted in order to prevent overfitting. We structured the GAMM to include the tensor product interaction between variables. To account both for temporal autocorrelation and for the dependency between observations collected on the same animal i , the model implemented the residual auto-regressive AR₁ correlation structure

$$\text{cor}(\varepsilon_{is}, \varepsilon_{it}) = \rho^{|t-s|}$$

applied to observations collected on each individual track at regularly spaced time-steps s and t . The generalized additive framework was adopted in order to account for nonlinearity between the response and the explanatory variables chosen.

2.4 Track simulation

For this analytical step, we only retained the transit bouts of the tracks. The last point of each transit bout interrupted by searching was connected to the first point of the subsequent transit bout by a beeline. These long, connecting segments were retained to preserve the trip configuration, but their duration and length were discarded from the final calculation of trip duration and distance travelled. The values yielded by the analysis therefore only refer to 'transit', rather than to the overall track.

We adopted four scenarios and generated the following simulated trips for each observed track: 100 random, 100 rotated, 1 reversed and 14 time-lagged simulated trips, all characterized by the same cumulative distance travelled as their respective real trip. To generate each random trip (figure 1b, top), we split the real trip into two legs, from the colony to the furthest away foraging location and vice versa, and within each leg all segments (i.e. all steps between GPS relocations) were randomly reshuffled. The rotated trips (figure 1b, bottom) were generated using a random rotate-shift model, fixed on the colony location, using the `adehabitatLT` package (Calenge 2016). The reversed trip had the same shape as the respective real trip, but the reverse direction, from the last GPS relocation to the first one. The time-lagged trips had the same route configuration as the observed tracks, but were shifted in time and had a timestamp delayed by 1–14 days,

resulting in different wind conditions at each location. Regardless of the method used, the duration of each simulated trip was calculated as follows. The start point of the real and random trips shared the same timestamp. Beginning from the start point 'a', we calculated the time required to travel to the following point 'a + 1' based on the step length predicted by the wind model given the wind conditions (Δ angle and wind intensity) experienced at 'a'. We then calculated the time of arrival at 'a + 1', extracted the local wind conditions at that time, and calculated the time needed to reach point 'a + 2'. This procedure was repeated for all points along the track until the endpoint 'e', and the cumulative duration of the trip was then calculated.

Finally, we focused on the homebound sections of each bird's track, i.e. from the furthest to the endpoint of the journey. From the furthest point 'f', we simulated a great-circle homeward 'beeline' trajectory, i.e. with the bird travelling heading directly to the colony. We calculated the hypothetical new wind conditions at 'f' and estimated how far along the beeline trajectory the bird would have moved in 2 h based on the wind model, defining a new point 'f + 1'. We repeated the calculation until the bird reached the endpoint, and extracted the cumulative duration and distance travelled.

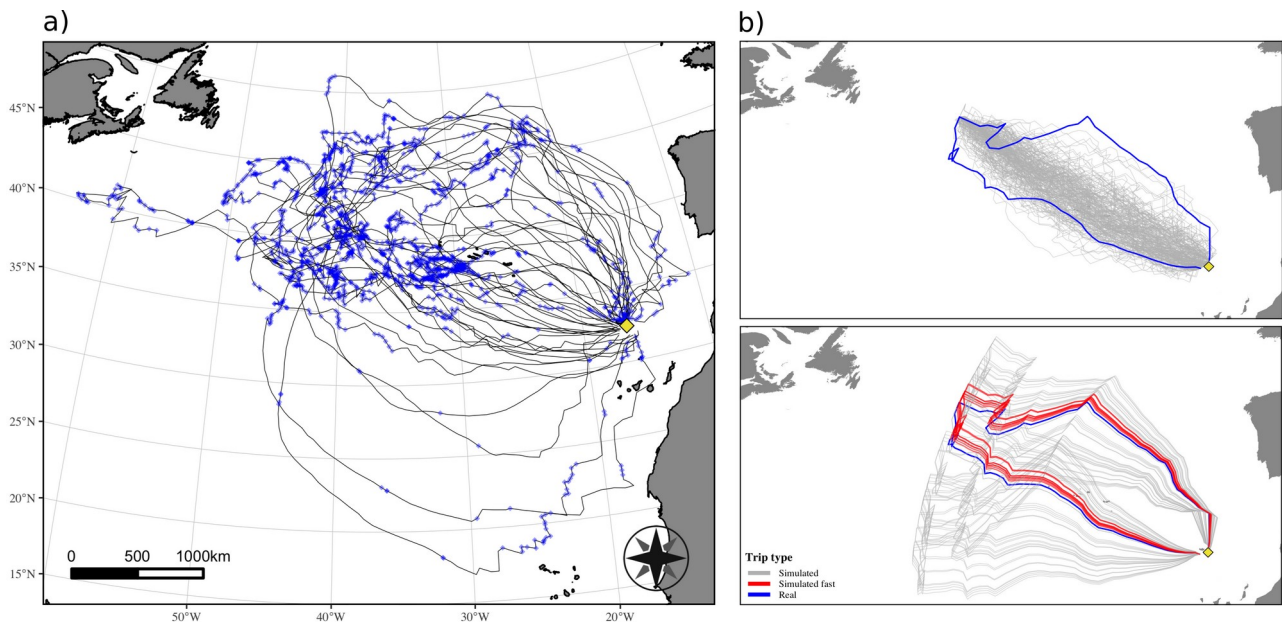


Figure 1 – (a) Desertas petrels' tracks. The blue dots represent the locations classified as 'searching'. The yellow rhombus shows the breeding colony on Bugio Island. (b) The random (top) and rotated (bottom) simulated trips based on an example track. The real trip is depicted in blue, the simulated ones in light grey. Of the rotated tracks, the ones that would grant the bird a higher mean speed are depicted in red. For clarity, only a subset of the 100 rotated tracks is displayed.

3. RESULTS

3.1 Spatial analysis

Desertas petrels undertook some of the longest foraging trips recorded for any animal species during breeding, almost reaching the continental shelf break waters off the coast of Newfoundland on a clockwise trajectory (figure 1a). On average they travelled for 14 (s.d. = 3.6) days, covering a total distance of 7891 (s.d. = 2205) km. The maximum trip duration and distance

travelled were 20 days and 12 000 km, respectively. Upon departure, they left the colony travelling west-southwest (circular mean bearing and circular variance equal to 262° and 0.16, respectively). When returning to their colony, the birds approached it from a northerly direction (circular mean bearing and circular variance equal to 182° and 0.22).

The best HMM model retained depth, distance from the colony, distance from seamounts and local time of day as significant predictors of the state switching probabilities. However, the inclusion of these explanatory variables affected the final classification only marginally: overall, only 2% of the total locations changed state after the inclusion of habitat covariates (supplementary material). Along the tracks, on average, 43% (s.d. = 15%) of the relocations were classified as searching. Transit and searching bouts had a median duration of 12h (interquartile range=6–20h) and 9h (interquartile range=4–16h), respectively. The overlap between individuals' foraging hotspots was 0.30. The overlap between individuals' travelling hotspots was equal to 0.49.

3.2 Wind use analysis

Overall, the Δ angle values exploited by Desertas petrels during transit (median= 60.7° ; interquartile range= 40.6° – 85.7°) and searching (median 68.9° ; interquartile range = 39.5° – 95.8°) were significantly different (figure 2a): in the linear mixed effects model with Δ angle as response variable and individual birds as random effects, the inclusion of behavioural state as explanatory variable was highly significant ($p < 0.001$). In particular, the transiting state was predicted to reduce Δ angle by an average of 4.3° . The results of the wind model showed that the ground speed of birds was affected by Δ angle in a nonlinear trend, with the predicted birds' speed peaking for values of Δ angle $\approx 50^\circ$. The model also showed that this trend was particularly emphasized when the birds were travelling with strong winds (figure 2b).

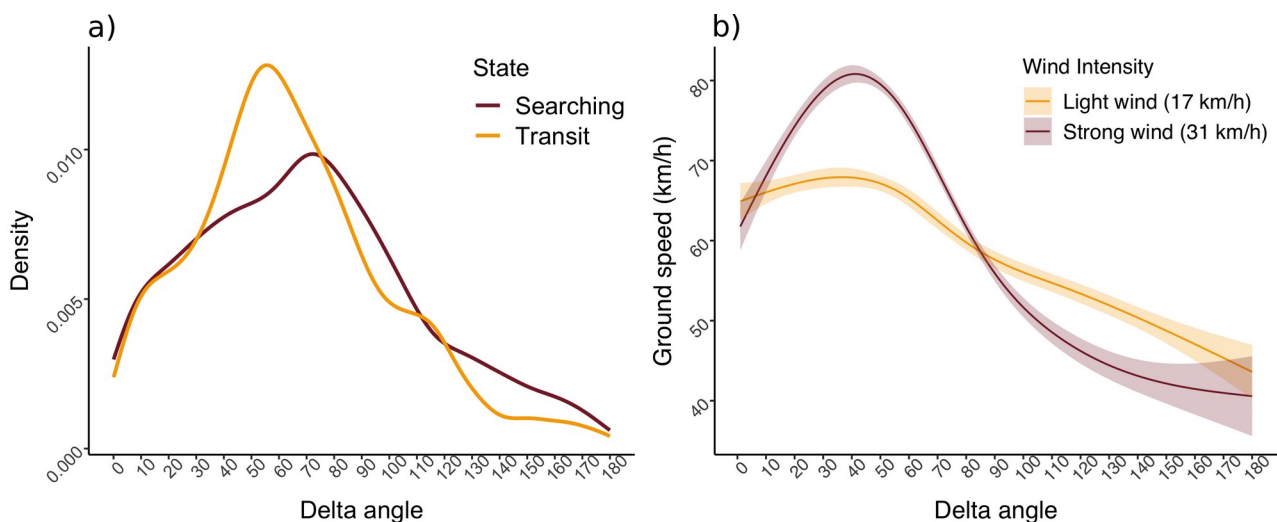


Figure 2 – (a) Density curves of Δ angle used by the birds along the tracks, separately for the searching and transit behavioural states. (b) Results of the generalized additive mixed effect wind model fitted to the transit portions of the tracks. The shaded areas represent the 95% confidence intervals. For visualization, the predicted effect of Δ angle on ground speed was calculated for light and strong winds (the 25 and 75% quantiles of the wind speeds experienced by the birds, equal to 17 and 31 km h⁻¹, respectively). The Δ angle predicted by the wind model to maximize the ground speed (50°) is similar to that maximally exploited by Desertas petrels during the transit state (60°).

3.3 Track simulation

Real trips were significantly faster than their equivalent simulated trips. This held true for random, rotated, inverted and time-lagged trips (figure 3). Real travel duration (mean= 180.3 h, s.d. = 59 h) was 27.3 h (i.e. 15.2%) shorter than the average duration of the respective random trips (paired t-test, $t = -4.37$, d.f. = 24, p-value < 0.001). The observed transit bouts were 16.9 h (i.e. 9.4%) faster than the respective average rotated trips (paired t-test, $t = -4.87$, d.f. = 24, p-value < 0.001). The few faster rotated tracks were in close proximity to the respective observed trip (figure 1b, bottom). The inverse trips were, on average, 65.2 h (i.e. 36.2%) slower than the corresponding real trips (paired t-test, $t = -7.82$, d.f.=24, p-value < 0.001). Finally, the real tracks were also significantly faster (by an average of 10.3 h, i.e. 5.7%) than the respective lagged trips (paired t-test, $t = -2.80$, d.f. = 24, p-value = 0.009).

Overall, the real homecoming portions of the tracks were 27.3 h longer (s.d. = 26.2 h) than the respective predicted beeline ones. By taking the observed homecoming route, birds covered 1201 km (s.d. = 794 km) more than they would have covered by travelling directly towards the colony. The mean travelling speed in the observed homecoming tracks was significantly higher (by 3 km h⁻¹) than the hypothetical speed attained in the beeline tracks ($t = 2.31$, d.f. =24, p-value = 0.03).

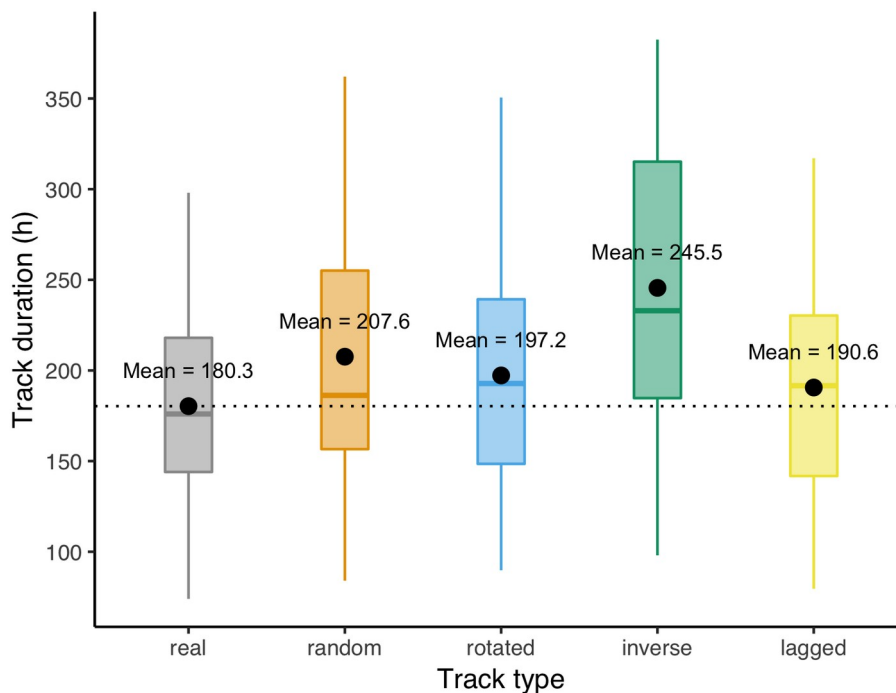


Figure 3 – Boxplot showing the track duration (in hours) of the real, random, rotated, inverse and time-lagged trips. The black circle represents the mean and the black dotted line shows the real tracks' mean. Real trips are significantly shorter than the respective random, rotated, inverse and time-lagged ones.

4. DISCUSSION

The gadfly petrels' impressive motility challenges our intuitive understanding of the central tenet of the optimal foraging theory, which predicts that animals should minimize foraging costs (in time and energy) and maximize energy intake. This is particularly true for Desertas petrels, which

do not target the highly productive waters in the Canary Upwelling system (Grecian et al. 2016) in proximity to their breeding site (potentially as a result of displacement due to competition or kleptoparasitism), but rather embark on their trips — among the longest in the animal kingdom — that take them thousands of kilometres away from their colony, into high-sea waters.

Owing to the petrels' high manoeuvrability, state-changes may occur over smaller scales than the temporal resolution of our data. However, on the one hand, during transiting, birds travelled at a ground speed of 33 km h^{-1} (s.d. = 8 km h^{-1} , see supplementary material for details), suggesting a fast, direct movement, which we expect the HMM to detect with a low rate of false positives. Importantly, as the ground speed calculation does not account for the sinuosity of the dynamic soaring flight within the 2h movement steps, the speed values are likely to be underestimated. On the other hand, while searching, the birds' ground speed was 14 km h^{-1} (s.d. = 8 km h^{-1}), excluding — at least for most of the movement step — the occurrence of transit behaviour. Thus, while acknowledging the limitation of inferring behavioural modes at 2 h resolution, we argue that the results of our analysis are robust and only minimally affected by the data coarse temporal resolution.

4.1 Hp1: birds exploit wind differently during the transit and searching states

During the transit phases of their trips, Desertas petrels most intensively travelled with a wind Δ angle of approximately 60° , similar to the value (approx. 50°) predicted by the wind model to maximize their ground speed. With this angle, wandering (Weimerskirch et al. 2000) and black-browed (Sakamoto et al. 2013) albatrosses were also found to travel at low energy expenditure per time unit. During the searching sections of their trips, birds showed a wind direction preference that peaked at higher Δ angle values (approx. 68°), i.e. for less favourable winds blowing more from the side. Interestingly, although the Δ angle selectivity during searching was lower (broader interquartile range), searching birds still showed a degree of wind selectivity. This supports the conclusion (presented below) that, when engaging in the searching activity, birds do not confine their search to specific areas, which would result in a higher variance of wind Δ angle used. Rather, they continue following their routes that allow a low cost movement, exploiting foraging opportunities encountered along the way. The differences in wind use between transiting and searching could be driven by a series of factors. Firstly, searching birds are predicted to make shorter, less directional (but see above) movements characteristic of the search behaviour, hence experiencing a wider range of Δ angle. Secondly, birds flying with less favourable winds can decrease their ground speed while still attaining adequate airspeeds to sustain flight, which could facilitate visual prey detection (Alerstam & Larsson 1993, Spear & Ainley 1997, Machovsky-Capuska et al. 2012). Thirdly, while looking for food, birds rely — to various extents — on odour plume detection, which in seabirds (Nevitt et al. 2008, Reynolds et al. 2015) and in a wide range of other animals (Vickers 2000, Cardé 2007) was found to benefit from orthogonal or oblique movements with respect to the direction of flow.

4.2 Hp2: during transit, birds fly with the most favourable relative wind direction

The wind model showed that the ground speed of transiting Desertas petrels was affected by wind relative direction, wind speed and their interaction, with greatest speeds attained when the birds travelled with strong, quartering tail winds (with Δ angle around 50°). Hence, our results revealed that transiting gadfly petrels efficiently exploit the wind fields, preferentially using quartering tail winds and thus maximizing ground speed. Seabirds flying with these favourable wind conditions were found to travel at minimum energetic cost (Weimerskirch et al. 2000, Sakamoto et al. 2013). Dynamic soaring and gliding, which characterize *Pterodroma's* flight and

are the least energetically expensive flight behaviour (Pennycuick 1982, Spear & Ainley 1997, Sakamoto et al. 2013), are indeed strongly associated with intense cross- and tailwinds (Ainley et al. 2015, Gibb et al. 2017).

4.3 Hp3: the foraging strategy is based on covering large distances to increase the probability of finding prey

The tracked birds search state occurred in waters that were on average deeper than 3600 m. The petrels performed 'looping' trips (Weimerskirch 2007), departing from the colony travelling southwest and returning from a northerly direction, a movement type — documented in pelagic species — suggesting a continuous search along the trip, which was explained in light of the food resources unpredictability at the coarse to meso-scale (Weimerskirch 2007). Desertas petrels' foraging hotspots were all located in deep, high-sea waters (supplementary material) and there was a limited among-individual foraging hotspots overlap compared with the travelling hotspots. Foraging site consistency in seabirds is related to predictability in marine resources, which are likely to be patchy and, at the coarse to meso-scale, unpredictable in the oceanic domain exploited by these birds (Weimerskirch 2007). Hence, to capitalize net energy gain, Desertas petrels seemed to rely on a foraging strategy based on covering large distances to increase the probability of encountering foraging opportunities along the route rather than consistently targeting known foraging areas (Weimerskirch et al. 2000, 2005). Our results corroborate and build mechanistically upon the findings of previous studies, in which breeding gadfly petrels were found to have a similar foraging strategy, with long foraging trips (Rayner et al. 2012, Ramírez et al. 2013, Ramos et al. 2017, Clay et al. 2019) characterized by low foraging site consistency (Clay et al. 2019), and long periods of direct flight (Rayner et al. 2012, Ramírez et al. 2013, Ramos et al. 2017, Clay et al. 2019), and in which birds travelling for longer distances had higher mass gains (Clay et al. 2019). It is important to note that the birds preferentially headed west when leaving the colony and used more intensely the waters in the region to the west-northwest of the Azores. This region is part of the North Atlantic Current and mid-Atlantic Subpolar frontal system (NAC-mASPF), characterized by the presence of thermal fronts and eddies and enhanced productivity at the large scale (Belkin & Levitus 1996, Rossby 1996). This suggests that, along their long and efficiently-designed routes, Desertas petrels did target a broad area of enhanced productivity, but at a large oceanic scale (greater than 1000 km²), continuously searching for food and maximizing the probability of prey encounter by covering more ground within this region and also while travelling to and from this region.

During the inbound phase of the journeys birds are more limited both in their choice of flight directions and in their remaining travelling time, as not only must they return to the colony, but also they must make sure to do so within the temporal constraints dictated by their parental duties (Stephens & Krebs 1986). However, we found that during the return section of the tracks, Desertas petrels do not fly towards the colony following a beeline, which would take them to the nest in a shorter time. Rather, they choose to undertake a longer route, characterized by better winds that enable them to fly at higher speed. This result, together with the HMM classification showing that the percentage of searching locations was similar in the outbound (46%) and inbound (41%) sections of the trips, strongly supports the idea that they continue looking for food also during the return phase of their journeys. To further increase the chances of encountering foraging opportunities, they keep travelling with favourable winds, selecting a longer path that allows them to cover more ground at high speed, also on their way back to the colony.

4.4 Hp4: travelling birds optimize their route to cover the largest distance in the shortest time by adjusting to regional and local wind conditions

The results on the random, inverse, rotated and time-lagged tracks offer further insight into Desertas petrels' flight behaviour. First, the clockwise observed tracks were faster than all their equivalent simulated trips. In particular, they were on average 65.2 h faster (i.e. more than one-third of the average duration of the observed tracks) than the respective inverse trips. Second, while the birds' observed route was significantly shorter than the corresponding rotated tracks, some rotated tracks near the observed trip would have granted the bird a slightly higher speed. Moreover, there was a high overlap between the individuals' travelling hotspots, indicating a significant extent of travelling route consistency among individuals. The selection of fast clockwise trajectories, the concentration of favourable simulated tracks around the observed one and the spatial consistency in the individuals' travelling routes all suggest that the predictable clockwise North Atlantic winds generate, at the large scale, predictable favourable flyways preferentially used by the birds. Furthermore, the real trips were significantly faster than the respective lagged tracks. In other words, if the observed trip were performed at another time — i.e. with different wind conditions — more time would have been required to complete it. This suggests that, while birds undertake trips that take advantage of a priori knowledge of the clockwise regional wind regimes prevailing in the North Atlantic, they are also capable of refining their route, adjusting it to the local wind conditions, in order to maximize their speed and distance travelled, ultimately maximizing the probability of finding prey.

5. CONCLUSIONS

Our research revealed new insights into the foraging strategy and flight behaviour of gadfly petrels, which are arguably the best performing flyers in the animal kingdom. These oceanic birds show a strategic use of wind, which enables them to travel at high speed and low cost. In turn, efficiently using winds allows them to exhibit a foraging strategy based on covering large distances while searching for food along the route rather than selecting specific foraging hotspots. Our findings suggest that the mechanisms at the core of this strategy, particularly advantageous in the oceanic marine domain, characterized by unpredictable resources distribution at the coarse to meso-scale, seem to be a prior knowledge of the — predictable — prevailing winds and the capability of efficiently refining their route to the local wind conditions. We argue that our quantitative analysis and our novel simulation framework can be successfully extended to reveal aspects of the ecology and movement behaviour of other wide-ranging animals moving through dynamic fluids such as air or water.

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SUPPLEMENTARY MATERIAL

1. The data

1.1 Tracking data

The tracking data were collected in the Desertas petrels colony in Bugio from 20 breeding adults during three consecutive breeding seasons (2015 to 2017). The tracked animals performed both long and short trips at-sea (fig. S1). As the role of these short movement bouts is uncertain – potentially not linked to foraging or involving a complementary foraging strategy – they might not be representative of the use of wind and foraging behaviour of Desertas petrels. We used k-means clustering (with 2 clusters for "short" and "long" tracks) to quantitatively distinguish between long and short tracks based on their maximum distance from the colony and total time at-sea using the Hartigan and Wong algorithm. The short movement bouts, mostly undertaken after the long journeys, were limited both in their temporal duration (average duration = 28 hours) and spatial extent (average distance from colony = 119 km) and overall, they represented only 13.7% of the total time spent at-sea by the tracked animals. We therefore removed the short trips from the analysis and retained a total of 25 long foraging trips (1 trip in 2015; 7 in 2016; 17 in 2017). All tracks from 2015 and 2016 were incubation trips, collected between August and the first half of September. Most trips from 2017 were incubation trips with the exception of 4 chick-rearing tracks, recorded between October and November. The data were collected using Pathtrack GPS devices programmed to store one location every 1 or 2 hours. The loggers weighted either 3.0 g or 7.4 g, and with added tape they represented less than 3% of the average body mass of a breeding adult recommended for seabirds (Phillips et al. 2003). They were attached with Tesa® tape on the four central tail feathers and retrieved from the tracked birds when they returned to the nest.

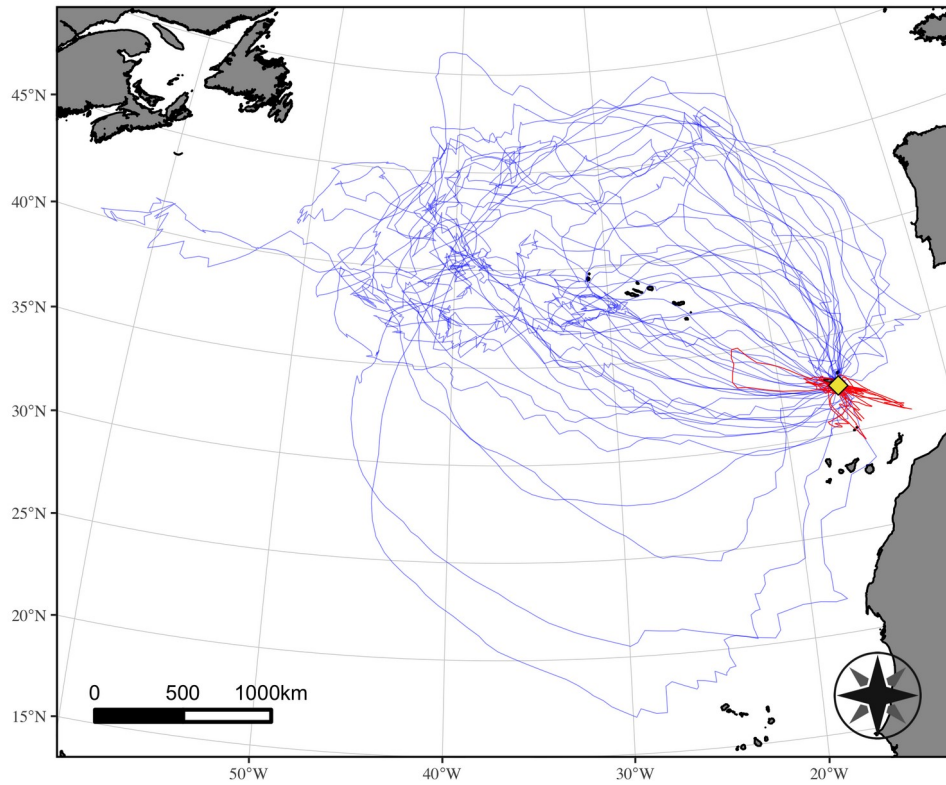


Figure S1 – Desertas petrels' long (in blue) and short (in red) tracks. The yellow rhombus is the breeding colony in Bugio Island. The short trips are limited both in their temporal duration (average duration = 28 hours) and spatial extent (average distance from colony = 119 km) and represent only 13.7% of the total time spent at-sea by the tracked Desertas petrels.

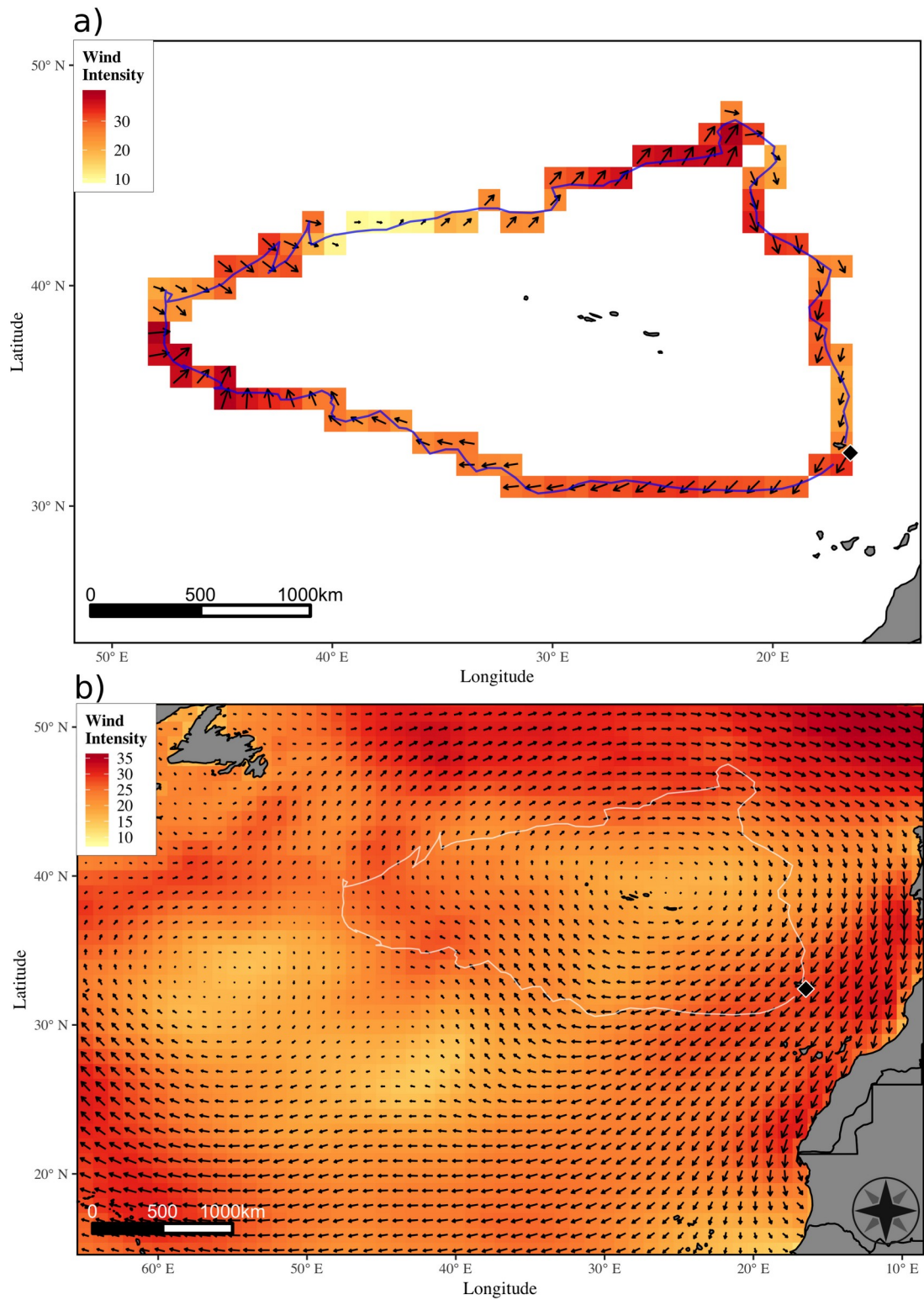


Figure S2 – The real-time wind conditions experienced along an example tracks (a) and the "overall" wind conditions, i.e. the wind direction and intensity averaged across the duration of the track (b). The tracked bird's trajectory followed the predictable prevailing clockwise winds (b), but

the animal also adjusted the track to the real-time conditions experienced en route (a), particularly evident in the northernmost portion of its trajectory.

1.2 Explanatory variables

We extracted a set of explanatory variables and associated them to the tracking relocations based on their coordinates and timestamp. The following environmental covariates were selected because we had an a priori hypothesis linking them (or a biological-oceanographic process for which they are proxy) and Desertas petrels state-switching probabilities (Table I). The physiographic variables downloaded were: depth (ETOPO Global Relief, at a spatial resolution of 0.017° , NOAA 2006); slope gradient and slope aspect ("slope" and "aspect", both expressed in degrees and calculated from the depth raster using the terrain function in the raster package in R). Weekly composite rasters for chlorophyll A concentration ("chla", expressed in mg/m^3) were downloaded from the NOAA VIIRS database, at a spatial resolution of $0.056^\circ \times 0.025^\circ$. The chla grids showed areas with missing values. Hence, prior to modelling, we filled the incomplete areas by interpolation using generalised additive models with thin plate regression splines in the mgcv package in R (Wood 2006). Sea surface temperature ("SST", expressed in $^\circ\text{C}$) grids were retrieved from the European Centre for Medium-Range Weather Forecasts (ECMWF, <http://apps.ecmwf.int/datasets/data/interim-full-daily/levtype=sfc/>), at a 3-hour temporal resolution and at a spatial resolution of 0.25° . The distance-related variables calculated were: distance from the colony ("distcol", in km) and distance from the closest seamount ("distseamount", in km, extracted from the Wessel's global seamounts map (Wessel 2001), only considering seamounts that are at a depth between 0 and 200 m), both at a spatial resolution of 0.017° . We computed the local time of day of each tracking relocation ("loctime"), accounting for the different time zones.

Table 1 – The covariates included in the model and the reason motivating their inclusion in the HMM model. The variable acronyms are defined in the text.

Variable	Reason motivating inclusion
Depth	Different prey distributed in shelf and oceanic waters. Desertas petrels mainly consume mesopelagic species. The animals are predicted to engage in searching behaviour in the bathymetric domain with higher preferred prey availability.
Slope	Slope areas are regions of water mixing, where nutrient-rich waters are forced towards the surface. We expect the animals' searching behaviour to concentrate in the more productive waters over the shelf (if preferred prey predictably aggregate over the slope areas).
Aspect	Slopes inclined differently interact differently with water currents and may or may not promote physical forcing of nutrient-rich waters towards the surface.
Chla	Index of primary productivity. More productive waters support higher densities of potential prey. We expect searching behaviour to occur more intensely in more productive waters with higher prey availability.
SST	Cooler waters forced to the surface are more rich in nutrients and support higher concentration of prey. We predict searching behaviour to be more strongly

	associated to cooler, more productive waters.
Distcol	Determines habitat availability for central place foragers. Once reached a critical distance, we expect the animals to be more likely to engage in the transiting mode to return back to the colony.
Distseamount	Near seamounts, physical forcing of nutrient rich waters towards the surface. The areas closer to seamounts grant the animals more foraging opportunities. Remain in or switch to searching behaviour in proximity of seamounts.
Loctime	Mesopelagic prey become accessible during specific temporal windows due to vertical migration in the water column.

Wind intensity ("wint", expressed in km/h), wind direction ("wdir") and tail wind component ("TWC", representing the wind speed component in the direction of flight, calculated as in Dell'Arciccia et al. 2018) were calculated from fine 3-hour temporal resolution wind grids were retrieved from ECMWF (<http://apps.ecmwf.int/datasets/data/interim-full-daily/levtype=sfc/>), at a spatial resolution of 0.25°. Finally, the difference in angle between the bird direction of movement and the wind direction (Δangle) was calculated following Wakefield et al. 2009.

$$\Delta\text{angle} = 360 - [\text{absolute value}(\text{bird bearing} - \text{wind direction})]$$

where bird bearing and wind direction were expressed using the same reference system.

2. Spatial analysis

2.1 Hidden Markov model

A state-space generalized multivariate hidden Markov modelling (HMM) framework was adopted to identify the behavioural states (searching or transit) of each bird along the track, based on the observed step lengths and turning angles. The model calculated the contribution of each environmental covariate to the state-switching probabilities. Moreover, different step lengths between observations reflect the true behavioural state of the animal, but in seabirds step length is also intrinsically dependent on the TWC experienced *en route*. Hence, within the HMM modelling formulation from the `momentuHMM` package in R (McClintock & Michelot 2018), we modelled the mean parameter of the state-dependent probability distribution of step length as a function of TWC.

Prior to model fitting, we ensured that the explanatory variables included in the full model were not collinear using variance inflation factors (VIFs). We used the `corvif` function in the `AED` package in R (Zuur et al. 2009), considering VIFs higher than 3 to be an index of collinearity. No signs of collinearity were detected. To facilitate model convergence, the continuous explanatory variables (with the exception of loctime and TWC) were standardised by subtracting the mean and dividing by the standard deviation. The distributions used to model step length and turning angle were a gamma and a wrapped Cauchy, respectively. We fit a full model to the state transition

probabilities, including the following explanatory variables: depth, slope, aspect, chla, SST, distcol, distseamnt and loctime (incorporated as a 24 hour cyclical pattern using the cosinor function). Additionally, using the DM (design-matrix) argument, we simultaneously accounted for the TWC effect on the on the mean of the state-dependent step length distributions for both states. A backwards model selection based on AIC was carried out on the full state transition probabilities model. We created a set of simpler models by iteratively removing a single covariate and calculated their respective AIC. The variable that caused the biggest drop in AIC was removed and the stepwise selection procedure was repeated until the removal of each variable caused the AIC to increase. Once the final best model was identified, the most likely sequence of hidden states was computed using the Viterbi algorithm (Zucchini & MacDonald 2009).

The probability distribution and parameter plots estimated by the HMM for the two states "searching" and "transit" are presented in figure S3. The step length (mean = 65.3 km in 2 hours; sd = 16.3) and the turning angle (circular mean = - 0.03 radians; circular variance = 0.09) for the transit behaviour both suggested a fast, direct movement. The searching behaviour was characterised by slower ground speeds (step length mean = 27.5 km in 2 hours; sd = 16.7) and more variable turning angles (circular mean = -0.06 radians; circular variance = 0.6). Interestingly, despite the higher variability in turning angles, the animals still showed a certain degree of movement directionality during the searching behaviour, further supporting the conclusions (presented in the main text) that, birds do not confine their search in specific areas, which would result in a higher turning angle variance, but rather, they continuously search along the track. The step mean parameter for both "searching" and "transit" was positively affected by TWC (fig. S3 b-c), with higher steps expected for higher TWC values, particularly during transit (but TWC had a marginal effect on the classification, see below). The final HMM model retained as significant the following explanatory variables: depth, distcol, distseamnt and loctime. The probability of switching between searching and transit was mostly driven by depth and distcol (fig. S4 a, b). As depth and distcol increased, the animals were more likely to show a transition from the searching to the transit state. Additionally, the variable distseamnt and loctime had a weak effect on the state transitions probability: the probability of engaging in searching increased as the animals flew closer to seamounts and when the local time was around 5 to 10 in the morning (fig. S4 c, d). However, the inclusion of the explanatory variables affected the final classification output only marginally. Compared to a model without explanatory variables, only 2% of the total locations changed state after the inclusion of habitat covariates.

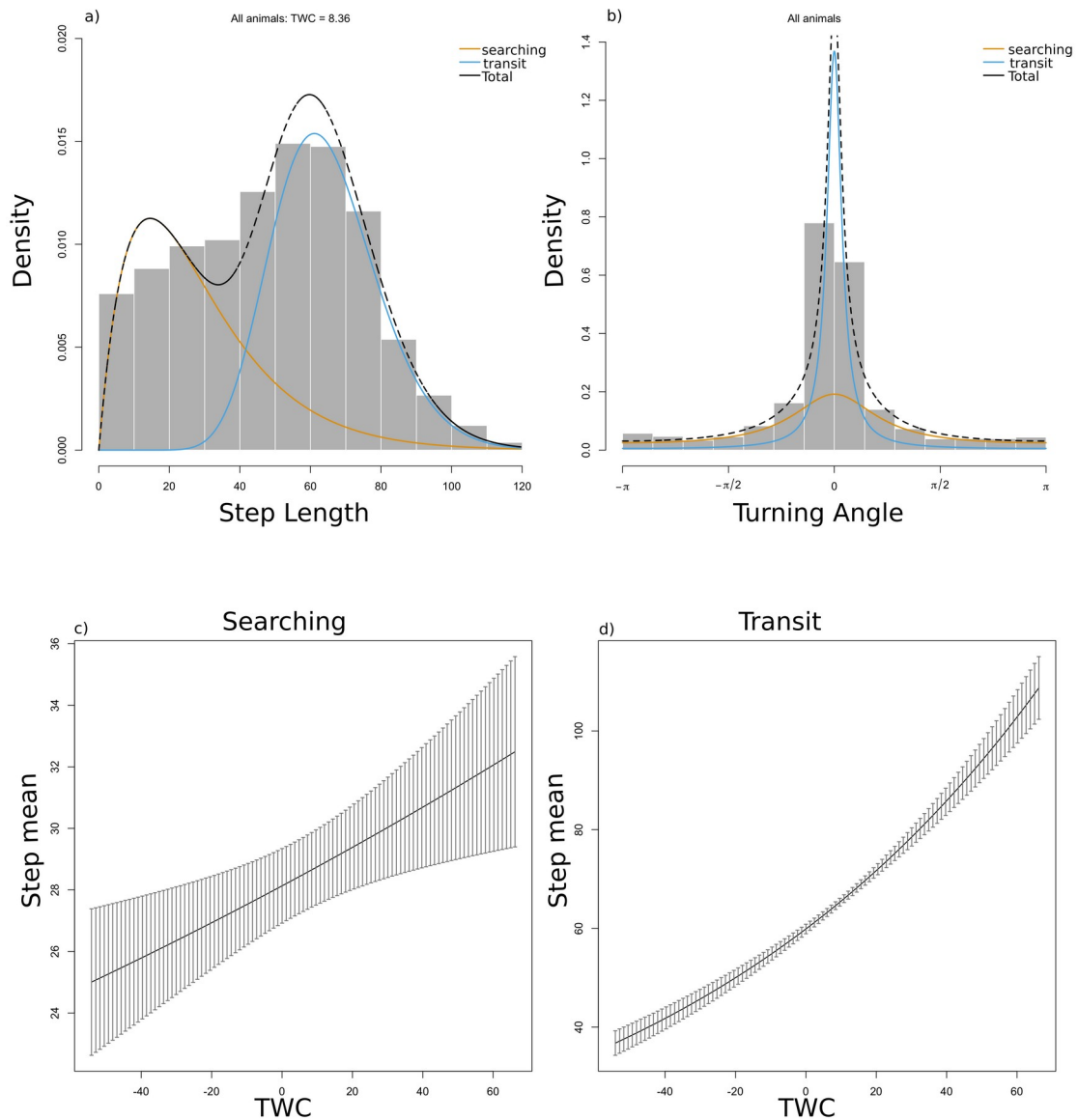


Figure S3 – Probability distribution and parameter plots estimated by the HMM for the two states "searching" and "transit". The panels represent histograms of the step length (a) and turning angle (b) data, with the solid lines showing the estimated state-dependent probability distributions. As TWC in the model design-matrix affects both states' step length mean parameter, the step length probability distributions are calculated for mean TWC values. Panels c) and d) present the estimated (with 95% confidence intervals) step length mean parameters of both states as a function of TWC.

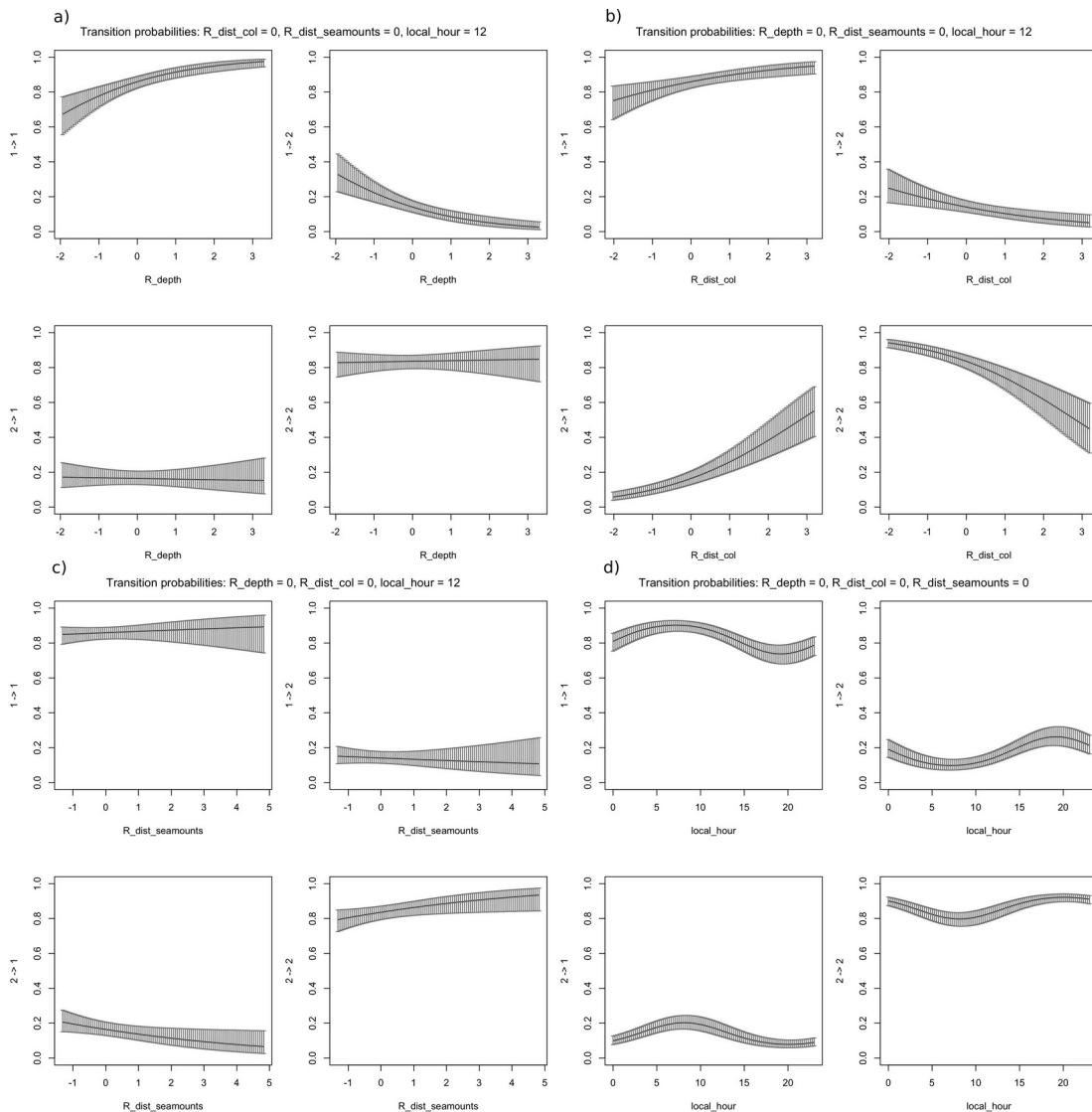


Figure S4 – The estimated effects of the model covariates on the state-switching probabilities (the covariates were standardised to help model convergence). Depth and distance from colony were the main drivers of the state switching probabilities. State "1" and "2" are "searching" and "transit", respectively. On the y axes, the notations "1 -> 2" and "1 -> 1", for instance, represent the probability of switching from "searching" to "transit" and of remaining in the "searching" state, respectively. As depth (panel a) and distcol (panel b) increased, the animals were more likely to show a transition from the searching to the transit state. Distance from seamounts (panel c) and local time (panel d) had a weak effect, with the probability of engaging in searching increasing as the animals flew closer to seamounts and when the local time was around 5 to 10 in the morning.

TWC was included in the HMM to improve the model's biological realism and to capture the intrinsic effect of wind on the animals' recorded step length (see section 2.2 Spatial analysis in the paper). However, overall, TWC had a marginal effect on the final classification output by the HMM. After reanalysing the dataset adopting a HMM that did not contain TWC in its design matrix formulation, less than 6% of the tracking points changed classification. Moreover, in order to assess the sensitivity of our GAMM results to the HMM design matrix formulation, we fitted the

wind model to the locations classified as transiting by the HMM that did not include TWC in its design matrix. The GAMM results obtained on the tracks decoded using this new HMM did not change, further highlighting that the HMM formulation does not affect the wind model results (figure S5).

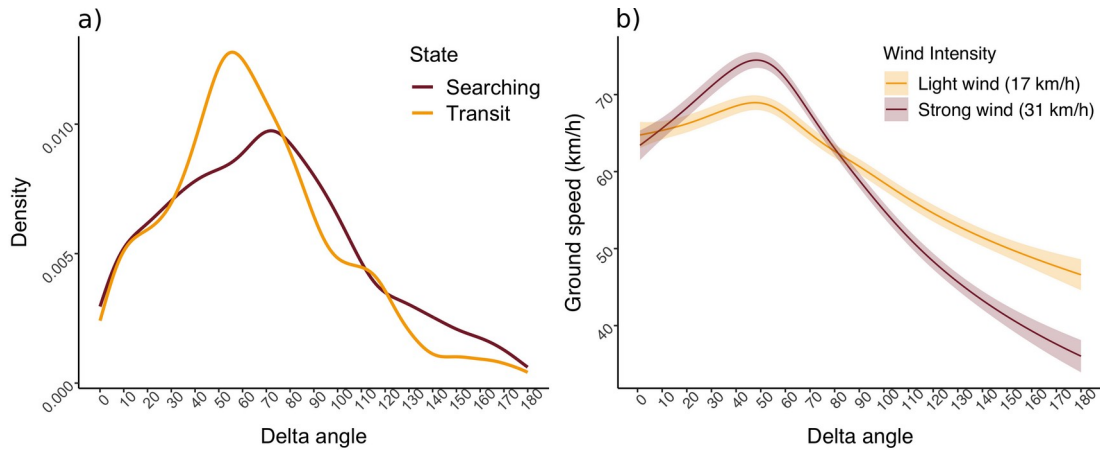


Figure S5 – (a) Density curves of Δ angle used by the birds along the tracks, separately for the searching and transit behavioural states. (b) Results of the generalized additive mixed effect wind model fitted to the transit portions of the tracks. The results showed are based on the HMM model without TWC in its design matrix. The results are only minimally different to those presented in the main text (see figure 2 in the main text). Hence, we argue that the HMM design matrix formulation does not affect the results and conclusions of our paper.

2.2 Foraging and travelling hotspots map

Two kernel Utilization Distributions (UDs) were constructed for each Viterbi decoded track based on the observations classified as searching and transit. UD were calculated using the kernelUD function in the R package adehabitatHR. The appropriate UD bandwidth was set to the overall maximum step length observed in a 2-hour interval (i.e. the observed maximum distance travelled within the tracks' temporal resolution). Following Ventura et al. 2019, for each state, we bootstrapped the sample of individual UD's obtaining 1000 re-samples, forcing the algorithm to select at least one individual from each year in each re-sampling iteration. For each bootstrap re-sampling round, the UD's were added together and normalised so that their sum was equal to 1. Thus, at the end of the process we obtained 1000 bootstrapped normalised UD's. Their mean was then calculated and we finally produced a map showing overall foraging and travelling hotspots (fig. S6).

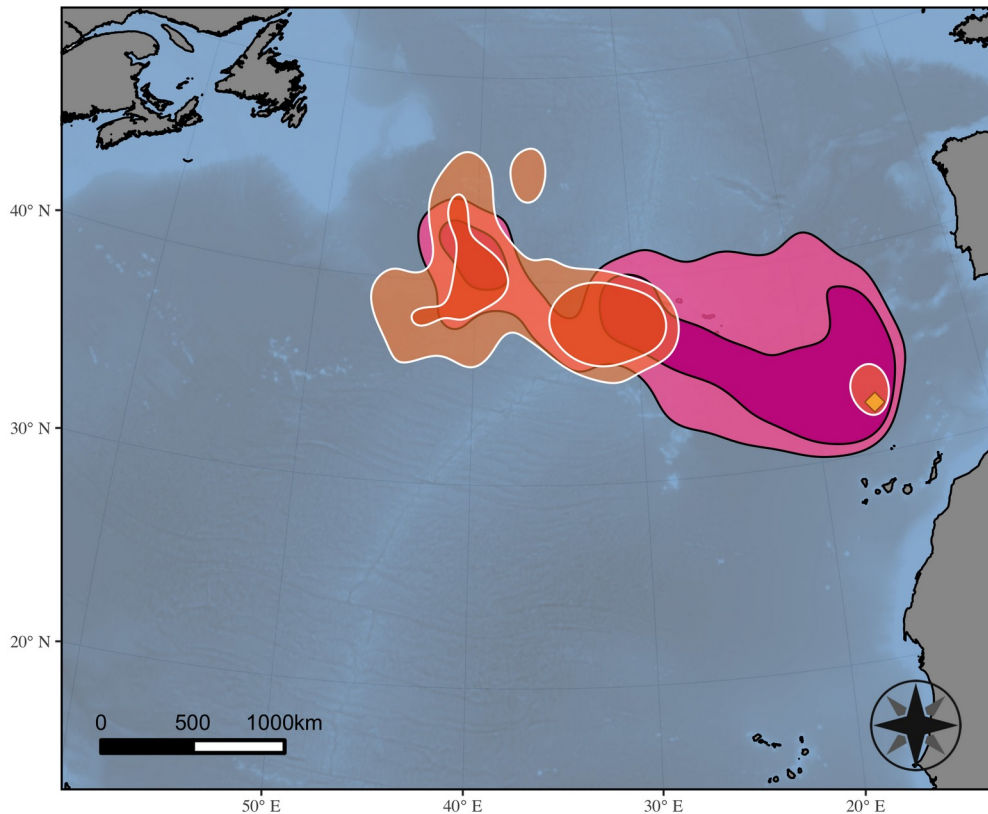


Figure S6 – The bootstrapped foraging (in orange) and travelling (in purple) Utilisation Distributions (UDs), computed based on the searching/transit locations estimated by the HMM. The 50% and 25% volume contours of each UD are showed in light and dark orange (searching) and light and dark purple (transit), respectively.

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CHAPTER 6

Central place foraging seabirds fly at right angles to the wind to jointly optimize locomotor and olfactory search efficiency

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Credits: Ben Metzger

ABSTRACT

Winds shape the central place foraging movements of seabirds. In predictable wind fields, seabirds should fly crosswind to maximize both the round-trip distance covered and the probability of detecting odor plumes. At present, however, there is no empirical evidence of this theoretical prediction. For the first time, we investigate the foraging movements of the Bulwer's petrel (*Bulweria bulwerii*) in the exceptionally persistent North Atlantic trade winds. We test the following hypotheses: in stable winds, petrels will fly at approximately 90° angles to the wind direction to maximize both the distance covered and the probability of detecting olfactory cues en route. We analyzed an unprecedented Bulwer's petrel GPS tracking dataset using state-space models and generalized additive models, and used Gaussian plume models to investigate how flight angle relative to wind impacts maximum detection distance of odor sources. Bulwer's petrels had the highest degree of selectivity for crosswinds documented to date, which often led to a systematic zig-zag flight, a behavior robustly documented here for the first time. Crosswinds maximized both the distance travelled and the probability of detecting odor plumes integrated across the round trip (rather than at any given point along the route, as this would result in energetically costly return flight). This evidence indicates that petrels plan the round trip flight at departure, integrating expected costs of the inward journey back to the nest. Our findings, likely true for other seabird species in similar ecological settings, further highlight the critical role of wind on the foraging ecology of seabirds.

Keywords

Central place foraging; flight behavior; olfaction; seabird; wind

1. INTRODUCTION

Animals should seek to minimize the energetic costs of movement during foraging while maximizing caloric intake to maximize net energetic gain (Krebs 1978, Nathan et al. 2008, Dickinson et al. 2010). Foraging strategies that maximize net energy intake take many forms depending upon a species' ecological niche and physiological and morphological adaptations. One very common constraint to bouts of foraging are found in species that must return to a "central place", usually to provide care for immobile progeny left at a rookery, nest, or den. Such species make foraging trips that last from a few minutes to a few days, but must return to the site the foraging trip originated from (Hamilton III & Watt 1970).

The foraging movements during breeding of seabirds are made from central places. This includes species from the order Procellariiformes (tube-nosed seabirds; the albatrosses, petrels and shearwaters), which arguably provide among the most fascinating examples of central place foraging. Members of this order spend most of their lives on the wing in the open ocean, returning to land only a few months per year to breed (Warham 1996). During breeding seasons, despite the constraint of a central place, foraging trips of seabirds can still cover thousands of kilometers (Ventura et al. 2020). This striking motility is underpinned by an exceptionally efficient flight strategy known as "dynamic soaring", whereby seabirds subsidize the greater part of locomotor cost of movement from the wind (Weimerskirch et al. 2000, Pennycuik 2002, Richardson 2011, Sachs et al. 2012).

The effect of wind on the costs of movement of central place foraging seabirds has been widely investigated from both theoretical (e.g. (Alerstam et al. 2019) and empirical (Spear & Ainley 1997, Weimerskirch et al. 2000, Ventura et al. 2020) perspectives. Dynamic soaring seabirds exhibit a movement orientation bias relative to wind direction ("anemotaxis"), flying at an advantageous angle relative to wind to maximize their traveling speed (Spear & Ainley 1997, Weimerskirch et al. 2000, Wakefield et al. 2009) and to minimize their energy expenditure (Weimerskirch et al. 2000, Sakamoto et al. 2013). Based on theoretical models, crosswind flight (i.e. at right angles to the wind direction) is predicted to be the optimal anemotactic strategy in a wind field that remains constant over the spatial and temporal domain of use (Alerstam et al. 2019). Moreover, owing to their capability of compensating for wind drift, birds exploiting constant and uniform winds should perform straight tracks (Chapman et al. 2011). These theoretical predictions are fairly intuitive, as birds flying with the assistance of advantageous tail winds during the outward section of the flight would have to face the costs of returning to the colony with headwinds. Due to the longer duration of the headwind homeward flight and the extra food load, the costs would exceed the benefits, making this strategy less profitable than crosswind flight (Alerstam et al. 2019).

In addition to its effects on movement and costs of locomotion, wind direction and intensity also greatly impacts advective odor dispersal, shaping the odor landscape on the surface of the ocean (Nevitt 2008, Nevitt et al. 2008). Perhaps unsurprisingly given their pelagic lifestyle, anemotaxis is a crucial mechanisms for olfactory foraging in procellariiform seabirds (Nevitt 2008). When searching for food, wandering albatrosses (*Diomedea exulans*) were found to fly using crosswinds and quartering sidewinds to maximize the probability of crossing an odor plume, and are able to detect odor sources at ranges of up to 20 km (Nevitt et al. 2008). Evidence of crosswind odor filament search strategies have been documented in other taxa, such as insects (Kennedy & Marsh 1974, Cardé & Willis 2008).

Thus, in stable and uniform winds, crosswind flight is predicted to be the most advantageous anemotactic strategy for seabirds to both minimize the energetic costs of a the combined outbound and inbound segments of foraging trips from central places, while also maximizing the number of odor plumes crossed for a given distance travelled. At present, no empirical observations have provided full support to these theoretical predictions and, in fact, for the reasons outlined below, key deviations from these predictions have instead been observed in other systems.

Historically, the geographical coverage of seabird tracking studies has been biased toward high latitude regions, which are characterized by much more variable wind conditions. Instead of using crosswind flight during the transit phase of their tracks, seabirds can carry out fast, long looping routes orienting at the most favorable angle with respect to the local wind conditions throughout the foraging trip (e.g. Weimerskirch et al. 2000). Use of wind fields by seabirds living in tropical and subtropical latitudes, where predictable trade winds prevail, is less well understood (Bernard et al. 2021), and there is scarcity of tracking data of dynamic soaring seabirds exploiting the stable trade winds found between 30°N and 30°S (Halley 1686). Secondly, tracking studies have also historically tended to focus on large seabirds able to carry heavy early generation tracking devices (Bernard et al. 2021). These large species are typically diurnal, feed on epipelagic prey, and show some levels of foraging site fidelity to predictable high productivity hotspots associated with seamounts, shelf breaks, upwelling regions and frontal zones, in which case the advantages of commuting to these areas may outweigh the sub-optimal energetic subsidies available during the commute from central places (Weimerskirch et al. 2000, Wakefield et al. 2009). Furthermore, upon reaching productive areas, seabirds may engage in area-restricted-search (ARS), performing

slower and more tortuous movement bursts (Nevitt 2008). During ARS, birds may deviate from a crosswind flight strategy by pursuing visual cues regardless of the wind conditions experienced, for instance, by directing their flight towards other foraging seabirds (Buckley 1997), fish schools, or fishing vessels (Nevitt 2000, Collet et al. 2015). Considerably less is known about the foraging ecology of smaller nocturnal seabirds feeding on mesopelagic prey. These birds may rely on visual cues to a minimal extent, feed opportunistically en route on less predictable food resources (such as vertically migrating prey present near the ocean surface mostly at night) and do not forage in large aggregations. These features suggest that they should maximally benefit from crosswind flight to facilitate olfactory food search.

Here, for the first time, we analyze the flight behavior and use of wind by foraging Bulwer's petrel (*Bulweria bulwerii*), a small (ca. 100g), nocturnal (Dias et al. 2016, Bonnet-Lebrun et al. 2021) specialist predator of mesopelagic prey (Waap et al. 2017) foraging in the persistent North Atlantic trade winds. The ecological features of this study system make it particularly well-suited for investigating the role of wind in shaping the movement patterns of petrels and other similar seabirds. Recent work using geolocation devices found that breeding Bulwer's petrels use waters both within and beyond the northern boundary of the trade winds belt (Dias et al. 2016). This feature thus provides enough environmental contrast to test if individuals adjust their flight strategy depending on whether their central place foraging trips are performed only in predictable trade winds or if their strategy changes when trips move beyond the trade winds belt and into less predictable wind fields. Specifically, we assess support for the following hypotheses:

H1) Birds performing central place foraging trips in persistent and predictable wind fields carry out trips orienting at 90° (orthogonally) to the prevailing trade winds. We predict that this preference for crosswind flights allows birds to maximize the distance covered per unit time (and minimize the energetic costs of locomotion) along the entire round trip. We also predict that, when birds use areas characterized by a higher variability in wind conditions, they sustain their trips exploiting a higher assistance by the wind (i.e. a higher tail wind component), when available.

H2) Birds performing crosswind flights maximize olfactory search information by optimizing the probability of detecting odor plumes. We predict that birds exploiting olfactory cues throughout their flight consistently show a preference for crosswinds both during day time (when visual cues can be used more extensively) and darkness (when visual cues are limited or absent). Flying at 90° to prevailing winds should maximize the distance at which a source can be detected and the overall area scanned using olfaction along the route.

2. MATERIALS AND METHODS

2.1 Data collection

We deployed GPS loggers on incubating Bulwer's petrels from colonies at Deserta Grande and Selvagem Grande (Madeira, Portugal) during three breeding seasons (June-July of 2015, 2016 and 2021). Tags were programmed to record locations on two schedules. In the first, loggers recorded points every hour, which allowed for analysis of flight throughout the entire foraging trips from the moment of departure to return and distinguish between "nearby" and "distant" trips. In the second, loggers recorded relocations every 3 minutes for six hours each day, which allowed for investigating wind use at a high resolution and with minimal chance of missed state-changes. Prior to analysis, all the tracks were linearly interpolated using the package *adehabitatLT* (Calenge

2016) in R software (R Core Team 2019) to impute missing data. The extent of interpolation was minimal (less than 2% of the points were imputed, see supplementary material).

The wind raster files were downloaded from the ECMWF ERA-5 database (<https://cds.climate.copernicus.eu/cdsapp>), at a spatial resolution of 0.25° and temporal resolution of 1 hour. The following variables were calculated for each GPS relocation: wind direction (in degrees), wind intensity (ms^{-1}), tail wind component (hereafter "TWC", calculated as in Dell'Araccia et al. 2018), and wind direction relative to the bird bearing (hereafter ' Δ angle', calculated as in Wakefield et al. 2009). Δ angle ranged from a minimum of 0° (tail winds, aligned with the direction of movement) to a maximum of 180° (head winds, blowing in the opposite direction of movement).

2.2 Movement analysis

We fit discrete-time hidden-Markov-models (HMMs) using the R package *momentuHMM* (McClintock & Michelot 2018) to classify the behavioral states of the petrels along the tracks, separately for the 1 h and the 3 min datasets. The most likely state sequence was inferred using the Viterbi algorithm (Zucchini & MacDonald 2009). We assumed that, along the 1 h resolution tracks, the petrels were in one of two behavioral states: "transit", in which the underlying drive is to move at high speed in a persistent heading; or "search", in which the drive is to search for food upon entering a foraging patch (Patterson et al. 2008). In the 3 min resolution tracks, we assumed that the petrels were in one of these three states: "in flight", when the birds spent the entire move step flying; "on water", when the animals spent the entire move step sitting on the water surface to ingest and process food or rest; and "mixed", an intermediate state in which the animals spent part of the step in flight and part on the water, indicative of foraging attempts (supplementary material).

2.3 Wind use analysis

The distribution of Δ angle for the different states in the 3 min and 1 h resolution tracks was calculated, quantifying separate Δ angle distributions for points recorded during day and night. The analysis subsequently evaluated the effect of wind on ground speed of the petrels. For this part of the analysis, we used only segments of the 1 h resolution tracks that were classified by the HMM as "transit". When birds were in this state, we assumed that the relationship between the wind and ground speed was only minimally affected by other activities, such as searching for food or resting. We fit generalized additive mixed effect models (GAMMs, hereafter referred to simply as "wind model") with the *mgcv* package (Wood 2006) in R to quantify the effect of Δ angle, wind intensity and their interaction on the ground speed attained by transiting petrels along the 1h resolution tracks. The best set of candidate variables to retain in the GAMM was selected based on AIC (Akaike 1998) (supplementary material).

2.4 Odor plume model

The objective of this analysis was to assess how the effective area searched using olfaction is affected by the Δ angle and wind intensity. To do this, we built Gaussian plume models (Holzbecher 2012), (hereafter referred to as "odor plume models") to analytically describe the wind-driven advection of odor plumes. We developed the odor plume model with constant emission rate from a source on the water surface, diffusivities along the y- and z-axis of $1000 \text{ m}^2 \text{ s}^{-1}$, constant decay and advection with the flow of a constant and uniform wind, and assumed that the birds could detect the smell when it decayed to 2×10^{-4} of the concentration measured at a distance of 1 m from the source. This choice yielded oval contour lines where the smell was

detectable up to a maximum distance from source of approximately 5 km, which is consistent with the detection distance documented in albatrosses (Nevitt et al. 2008). A set of odor plume models and resulting oval smell detection contour lines were generated with wind intensities ranging from 1 to 15 ms^{-1} . Then, integrating the results from the odor plume model with the predictions from the wind model (i.e. the predicted ground speed attained at a given Δ angle and wind intensity), we calculated two key quantities. First, the theoretical "olfactory bandwidth", i.e. the maximum distance from the source at which the birds are predicted to detect a smell, for each value of Δ angle and wind intensity, calculated applying trigonometric formulae (fig. 1). Second, the theoretical area olfactorily scanned (km^2) by a bird flying at a given Δ angle and wind intensity during one movement step (1 hour), calculated by multiplying the olfactory bandwidth by the predicted distance covered (supplementary material). A sensitivity analysis was carried out, which showed that the results obtained on the effects of Δ angle and wind intensity on the area scanned are robust to the parameter specification (supplementary material).

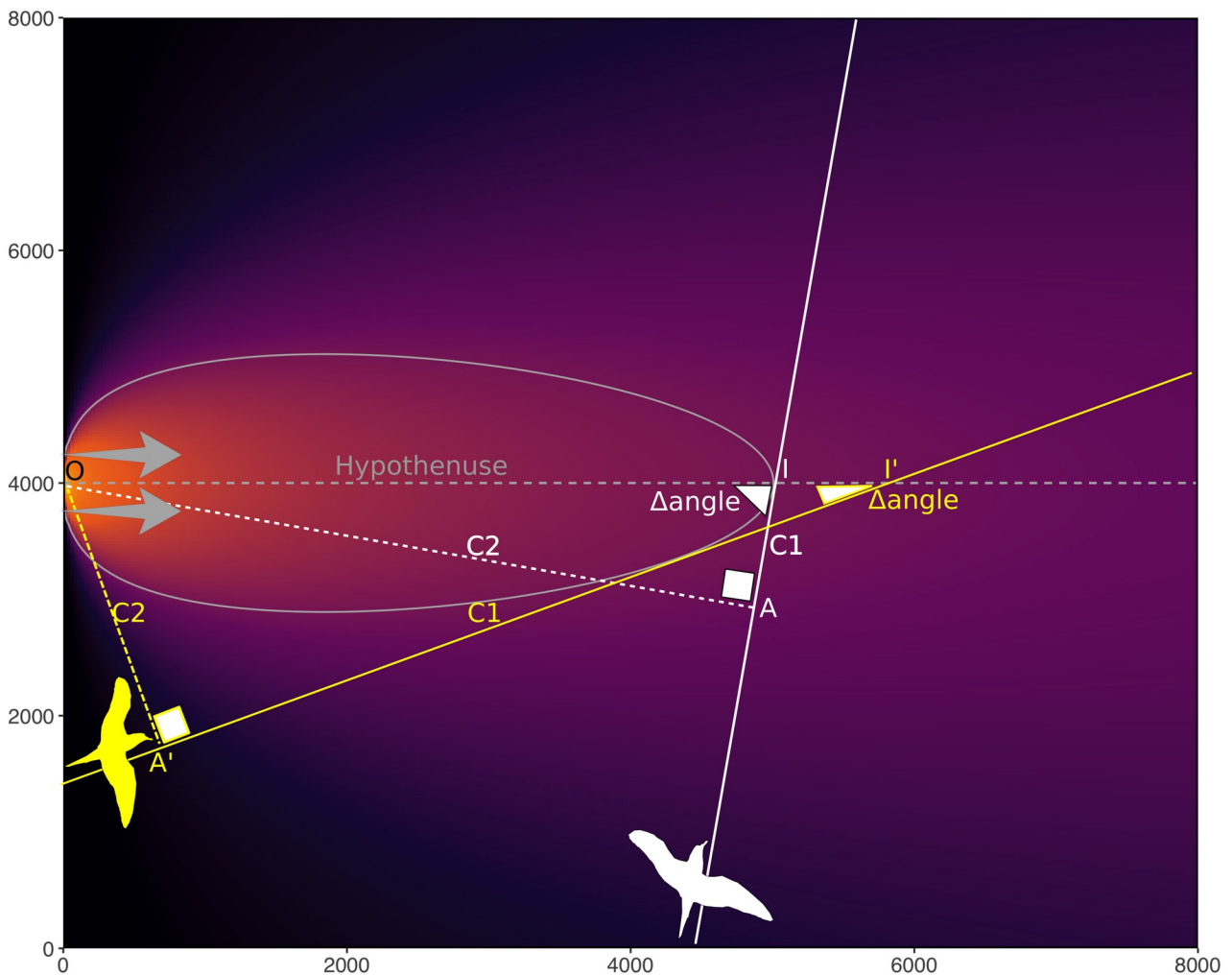


Figure 1 – The smell detection contour generated by the "odor plume model". The constant and uniform wind is represented by the central arrows. The smell source is at "O". The x and y axes are expressed in meters. Two potential trajectories are depicted, with birds flying at two Δ angle values: 10° and 80° (yellow and white solid lines, respectively). Two right triangles are obtained, delimited by: the hypotenuse (OI' and OI for Δ angle of 10° and 80° respectively); the cathetus "C1" adjacent to Δ angle (A'I' and AI, adjacent to the Δ angle of 10° and 80°); and the cathetus "C2" opposite to Δ angle (OA' and OA). C2, calculated as $C2 =$

hypotenuse * $\sin(\Delta\text{angle})$, is the "olfactory bandwidth", i.e. the maximum distance from the source at which a smell can be detected.

2.5 Track simulation: distance covered and area scanned

We applied a simulation framework to investigate whether, along the realized trips, birds: 1) maximize their speed; and 2) maximize the area scanned using olfaction along their entire round-trip foraging route from a central place. In short, a set of "random" and "rotated" simulated tracks were designed, which were equivalent (i.e. covering the same distance) to their corresponding real tracks, but along these simulated routes the birds travelled at a different Δangle . We compared the duration and the area olfactorily scanned along the simulated trips to the duration and area scanned throughout the real trips (supplementary material).

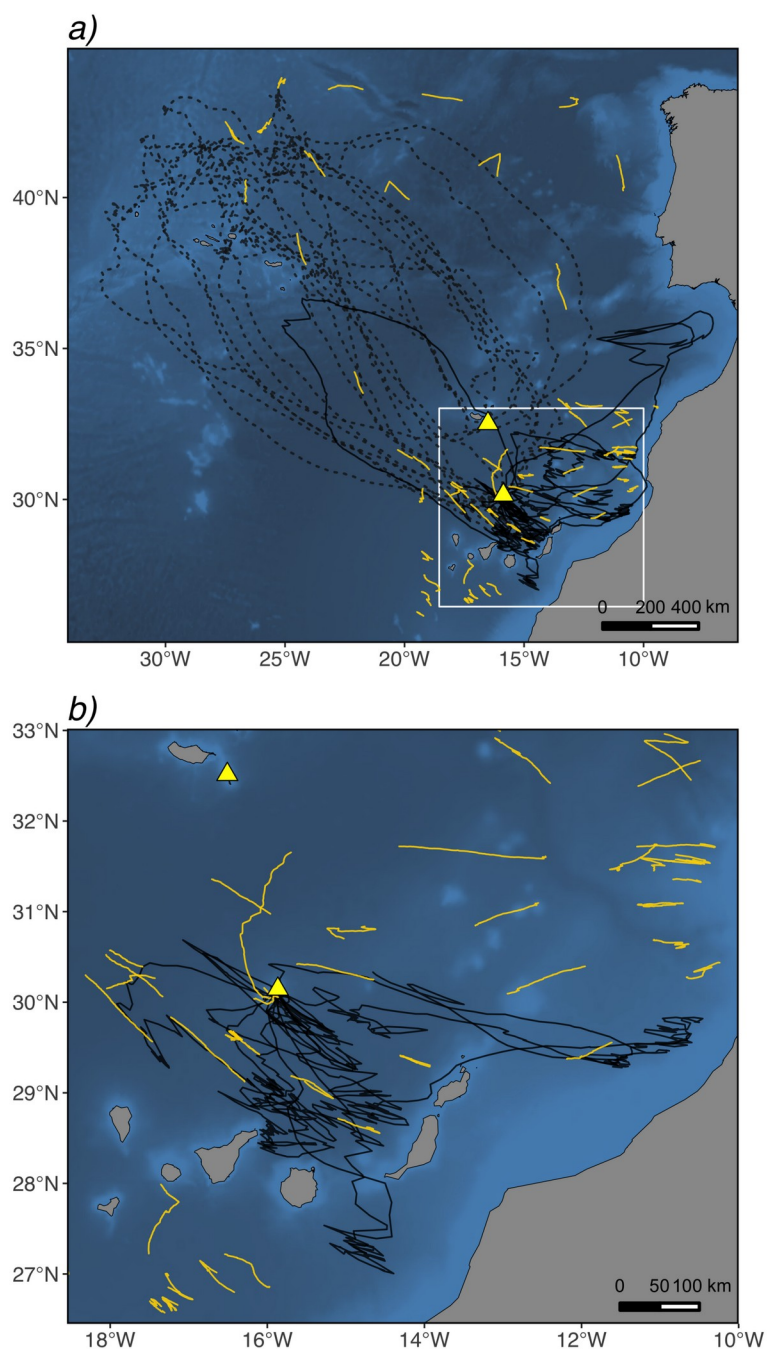


Figure 2 – (a) All tracks, both at 3 min (in gold color) and at 1 h resolution (in black) are depicted. The "distant" and "nearby" 1 h resolution trips are represented using dotted and solid lines, respectively. The white rectangle depicts the extent of panel (b) below. (b) A selection of 1 h and 3 min resolution tracks (in black and gold colors, respectively), highlighting the zig-zag flight performed by the petrels. The triangles represent the colonies.

3. RESULTS

3.1 Movement analysis

Two high-usage areas were identified: a "nearby" area, located off the coasts of the Canary islands and West Africa, within the trade winds belt; a "distant" area, encompassing the waters to the northern edge of the trade winds belt and beyond, to the north of Azores, reached by the birds through clockwise looping trips (supplementary material). The tracks showed a high degree of movement directionality. The birds mostly flew at constant heading between few sharp turning points, resulting in a series of zig-zagging trajectories. This is evident both in the 1 h resolution tracks (particularly off the coasts of the Canaries and West Africa, but also near the coasts of the Azores) and in the 3 min resolution tracks (fig. 2), in which the petrels often did not change heading during the whole duration of the 6 hour segments. On average, the complete 1 h resolution foraging trips of Bulwer's petrels ($n = 18$ complete tracks) lasted 11.52 days (s.d. 1.78 days). The average total distance travelled was 4143.60 km (s.d. 981.45 km) and the average maximum distance from the colony was 1137.93 km (s.d. 605.05 km). The maximum distance from the colony was not significantly correlated with the temporal duration of the trips (Pearson's correlation, $r_{16} = -0.04$, $p = 0.89$). An average of 52% (s.d. = 18%) of the relocations were classified as searching. Overall, both the sections of the tracks classified as transit and search were characterized by a high degree of movement directionality. Specifically, the mean turning angle was equal to -0.38° (circular standard deviation = 30.82°) for the transit state and -1.35° (circular standard deviation = 76.34°) for the search state. The average speed during transit was 22.22 kmh^{-1} (s.d. = 5.46 kmh^{-1}) whereas birds in the search state flew at an average speed of 9.06 kmh^{-1} (s.d. = 6.05 kmh^{-1}). Along the 3 min resolution tracks (fig. 2) the average ground speed was equal to: 26.4 kmh^{-1} (s.d. 7.19 kmh^{-1}) when birds were in flight; 3.14 kmh^{-1} (s.d. 3.46 kmh^{-1}) when they were on the water; and 19.5 kmh^{-1} (s.d. 5.50 kmh^{-1}) when they were in the "mixed" state. The 3 min resolution tracks also showed high movement directionality. Specifically, the turning angle of the birds was equal to 0.14° (circular standard deviation = 20.76°) when in flight; -0.41° (circular standard deviation = 70.52°) when the birds were sitting on the water; and 0.54° (circular standard deviation = 28.89°) when the birds were in the "mixed" state.

3.2 Wind use analysis

The petrels exhibited an extreme degree of selectivity for crosswinds (table I and fig. 3). This was evident both during the "in flight" and the "mixed" sections of the 3 min resolution tracks, but also along the "transit" and "search" sections of the 1 h resolution trips, resulting in strikingly narrow Δ angle density curves, particularly compared to the wind use of other seabirds in the region (fig. 3b). When "in flight" along the 64 tracked flight bouts at 3 min resolution, petrels mostly flew orienting almost perfectly orthogonally with respect to the wind (median Δ angle = 89.90°), spending 64% of their "in flight" time flying at Δ angle between 70° and 110° . Similarly, when in the "mixed" state, they used crosswinds, flying at a median Δ angle of 85.85° (table I and fig. 3a). The wind use along the 1 h resolution tracks (comprising a total of 22 trips, of which 9 "nearby" and 13 "distant") is largely consistent with the findings described above (particularly so for the

"nearby" trips). The petrels showed a preference for crosswind flight, both during the transit and the search state (table I and fig. 3b). The Δ angle used by the birds along the "nearby" and "distant" 1 h resolution trips was significantly different (Mann-Whitney-Wilcoxon Test, p -value < 0.001). The petrels had a higher selectivity for crosswind along the nearby trips, whereas their wind use shifted towards more quartering tailwinds during the distant trips (table I). Moreover, the TWC experienced along the nearby and distant trips was different (Mann-Whitney-Wilcoxon Test, p -value < 0.001). Along the distant trips the birds travelled with a stronger support by the wind (median TWC = 1.87 kmh^{-1} ; interquartile range= 0.12 – 3.72 kmh^{-1}) compared to the nearby tracks (median TWC = 0.16 kmh^{-1} ; interquartile range= -1.86 – 1.77 kmh^{-1}). Overall, the birds consistently used crosswinds along the 3 min resolution tracks, both during day and night (table I), resulting in Δ angle values not significantly different during light and darkness (Mann-Whitney-Wilcoxon Test, p -value = 0.51). This result was also true for the 1 h resolution tracks (Mann-Whitney-Wilcoxon Test, p -value = 0.54) (table I).

The results of the wind model based on the locations classified as "transit" showed that, at each movement step, the petrels are predicted to attain highest ground speed with favorable tail to quartering winds. Specifically, the wind model retained Δ angle, wind intensity and their interaction as significant predictors of ground speed. The ground speed was non-linearly affected by Δ angle and wind intensity, with a maximum speed attained by the birds at values of Δ angle $\approx 30^\circ$, particularly when traveling with stronger winds (fig. 4a). The results of a wind model fitted to the 3 min resolution tracks are largely consistent (supplementary material).

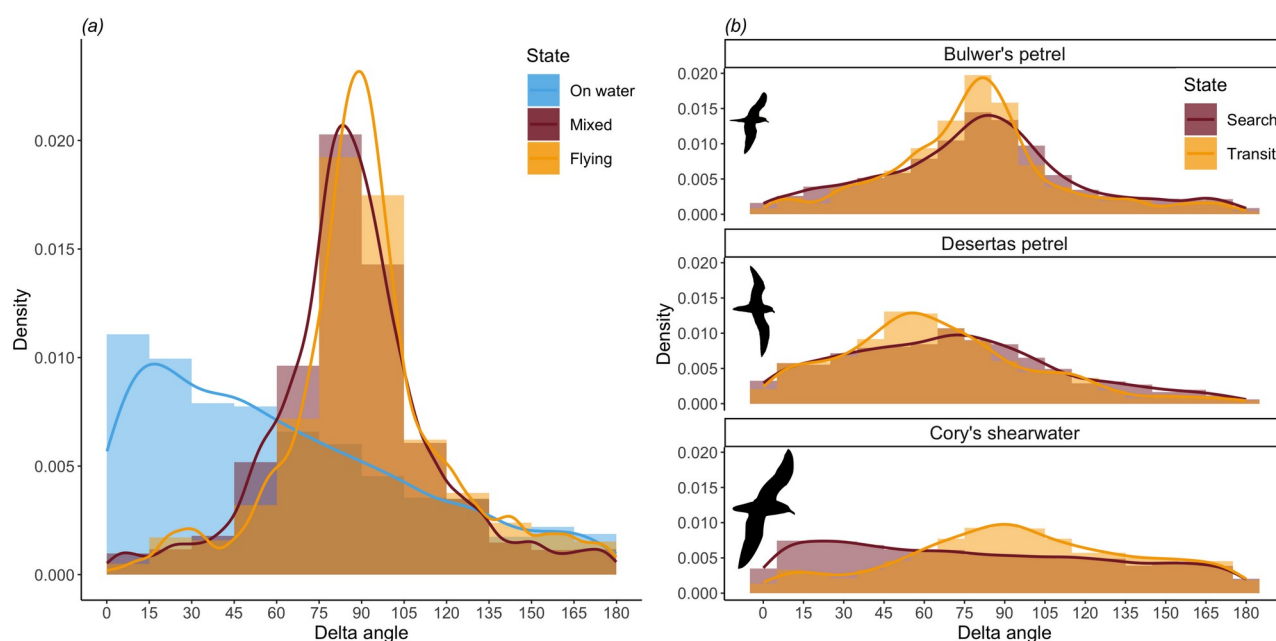


Figure 3 – (a) Density curves of Δ angle used by the Bulwer's petrels along the 3 min resolution tracks. Different colors are used to represent the different behavioral states. (b) The Δ angle used by Bulwer's petrels along the 1 h resolution tracks during "search" and "transit" (in the top panel) is compared with that used by Desertas petrels ($n = 25$ tracks) and Cory's shearwaters ($n = 103$ tracks).

3.3 Odor plume model

For all wind intensities, the olfactory bandwidth ("C₂" in fig. 1) is maximum for Δ angle values of 90° (fig. S₄ in supplementary material). At low wind intensities, when the predicted effect of wind

on the ground speed of the petrels is minimal, a Δ angle of 90° maximizes the area scanned (km^2 in 1 h) by the olfactory searching birds (fig. 4b). As the wind intensity increases, the oval smell detection contour becomes stretched along the direction of wind flow (fig. S3 in supplementary material). Furthermore, for increasing wind intensities, the birds are predicted to attain higher speeds with favorable tail to quartering winds, whereas the use of crosswinds results in lower speeds. In turn, at intermediate (e.g. 7 ms^{-1} , which is the average wind intensity experienced by the petrels along the 1 h resolution tracks) and high (e.g. 15 ms^{-1}) wind intensities, the peak of the theoretical area scanned shifts towards Δ angle values $< 90^\circ$ (between 60° and 65° , fig. 4b).

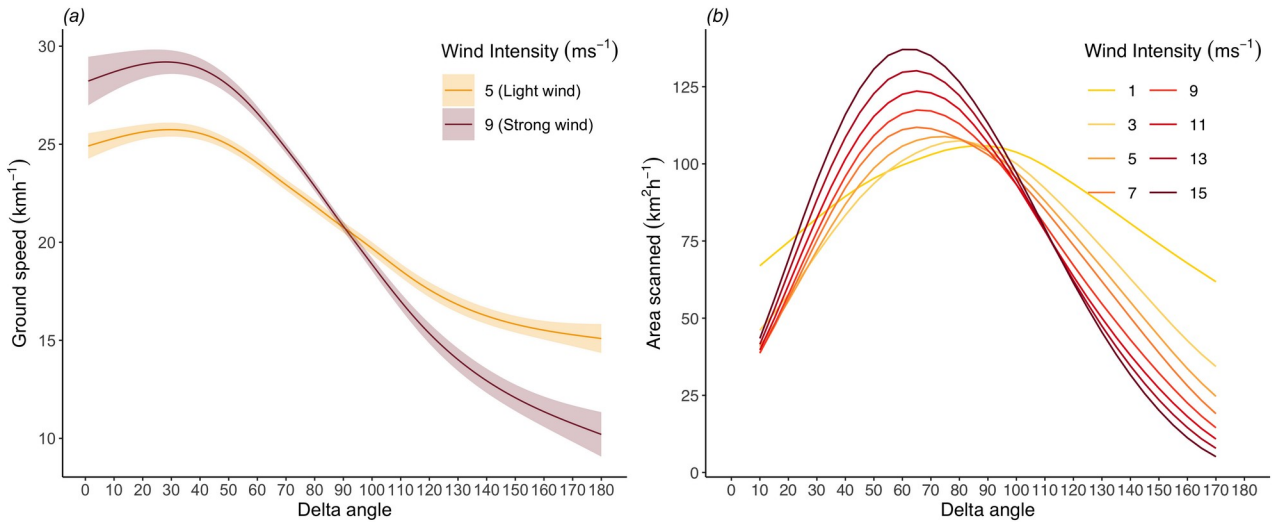


Figure 4 – (a) GAMM "wind model", fitted to the transit segments of the 1 h resolution trips. The 95% confidence interval is represented by the shaded areas. For visualization purpose, the predicted effect of Δ angle on ground speed (kmh^{-1}) was calculated for light (5 ms^{-1}) and strong (9 ms^{-1}) winds. (b) The theoretical area olfactorily scanned (km^2 in 1 hour), as a function of wind Δ angle and wind intensity.

Table 1 – The median and interquartile ranges of wind direction relative to the bird bearing (" Δ angle") quantified for the different track sections and temporal resolution.

Trip (resolution)	Section	Δ angle, median	Δ angle, 25%–75% interquartile range
Overall (3 min)		85.30°	65.96° – 101.04°
In flight (3 min)		89.90°	77.94° – 103.36°
Mixed (3 min)		85.85°	72.58° – 100.39°
On water (3 min)		52.19°	22.99° – 92.45°
Day (3 min)		85.42°	65.54° – 101.67°
Night (3 min)		84.80°	67.74° – 98.73°
Overall (1 h)		80.03°	58.92° – 96.35°

Transit (1 h)	79.04°	60.33°–92.71°
Search (1 h)	81.16°	57.67°–100.01°
Day (1 h)	80.14°	57.91°–97.33°
Night (1 h)	79.85°	61.36°–94.31°
Nearby (1 h)	88.81°	76.95°–104.64°
Distant (1 h)	72.02°	49.07°–88.81°

3.4 Track simulation: distance covered and area scanned

The real tracks realized by the transiting petrels were significantly faster than the random (paired t-test, $t = -5.03$, d.f. = 17, p -value < 0.001) and rotated trips (paired t-test, $t = -3.66$, d.f. = 17, p -value = 0.002). The real duration was, on average, 175 h and 211 h (i.e. 136% and 164%) faster than the duration of the respective random and rotated trips. The area scanned throughout the real trips was also significantly wider than the area scanned along the random (paired t-test, $t = 3.11$, d.f. = 17, p -value = 0.006) and rotated (paired t-test, $t = 7.35$, d.f. = 17, p -value < 0.001) tracks. More specifically, the area scanned along the real trips was on average 646 km² and 1304 km² (i.e. 5% and 11%) wider than the area scanned along the respective random and rotated trips (fig. S6 in supplementary material).

4. DISCUSSION

Bulwer's petrels have a higher degree of selectivity for crosswinds than any other seabird tracked to date. This strategy, exhibited both when in transit and searching, and consistent across different observation resolutions of our tracking dataset, is striking if compared to the wind use of other seabird populations from the same region (fig. 3b and supplementary material). Our results show that crosswind flight enables the birds to maximize both the distance covered and the area olfactorily scanned throughout their trips. Furthermore, for the first time, we document an emerging property (discussed below) of the central place foraging trips of the petrels, underpinned by the high selectivity for crosswinds: a systematic zig-zag flight, both during the transit and the search sections of their tracks.

4.1 Crosswind flight to maximize distance covered in stable winds

Our results provide strong empirical support for the hypothesis that crosswind flight allows petrels to maximize the distance covered throughout their central place foraging routes (H₁). Bulwer's petrels are predators of mesopelagic prey (Waap et al. 2017) that do not consistently target predictably rich foraging hotspots (Dias et al. 2016). Rather, they forage over deep oceanic waters on unpredictable prey at coarse (1–100 km²) and meso scales (100–1000 km²), covering as much distance as possible in order to maximize the probability of opportunistically find prey along their routes.

Here we clearly show that crosswind does not maximize the ground speed along each movement step. As predicted by the wind model, birds fly the fastest with quartering-tail winds, which aligns

with the findings on the speed and energy expenses of other dynamic soaring seabirds, such as albatrosses and gadfly petrels (Weimerskirch et al. 2000, Sakamoto et al. 2013, Ventura et al. 2020). Rather than representing a strategy to maximize their instantaneous speed, Bulwer's petrels use crosswinds to maximize the distance covered along their entire round trips from central places carried out in predictably stable wind fields. This anemotactic strategy is different than, for instance, that of gadfly petrels (e.g. Desertas petrels, *Pterodroma deserta*), which design fast long tracks consistently selecting a wind Δ angle that enable them to maximize their speed (Ventura et al. 2020). Compared to the larger gadfly petrels, Bulwer's petrels are smaller, fly at a lower ground speed and have lower wing loading and aspect ratio (Spear & Ainley 1997). These anatomic features make headwind flight particularly disadvantageous (Spear & Ainley 1997) and potentially unsustainable and, in fact, the petrels only extremely rarely engaged in headwind flight.

The tracked petrels were also found to travel beyond the trade winds belt, carrying out long clockwise routes. Rather than commuting to distant foraging hotspots, we argue that the benefit of such longer trips may be the higher distance covered to increase the probability of encountering food en route. In line with previous evidence (Dias et al. 2016), we found that the Bulwer's petrel foraging range was not correlated with the temporal duration of their journeys owing to the higher average speed along the distant trips than along the near trips, underpinned by the use of comparably more advantageous wind Δ angles. By exploiting a higher variability in winds, petrels consistently chose more favorable Δ angles and received a higher assistance by the wind (i.e. higher TWC) along the distant trips, resulting in the longer commutes being significantly faster than the respective simulated trajectories. All these findings strongly suggest that Bulwer's petrels rely on an impressive knowledge of the regional wind availability and real time wind fields. When birds stay within the stable and more predictable trade winds region, they use crosswinds to cover as much distance as possible along the entire route, a strategy that will prevent them from performing long headwind commutes on the way back. Such selection for integrated optimization over the course of multi-day return route from a central place suggests that, upon departure, these animals may plan their overall route across that entire period, and anticipate the expected winds that they will experience days later when they return to the colony.

4.2 Crosswind flight and area scanned using olfaction

In line with previous evidence (Nevitt et al. 2008), we found that crosswind flight enables the birds to maximize the olfactory bandwidth, supporting H2, consistently across all wind intensities. At low wind intensities, crosswind flight (i.e. a Δ angle values $\sim 90^\circ$) maximized both the olfactory bandwidth and the theoretical area scanned. However, for higher wind intensities (the typical wind intensity in the study area is $\sim 7 \text{ ms}^{-1}$), petrels using crosswinds attained lower ground speeds than birds using quartering-tail winds. In turn, for a range of stronger winds, the theoretical area scanned was maximized for wind Δ angle values smaller (between 60° and 65°) than the preferred Δ angle ($\sim 90^\circ$) most intensely selected by the petrels. Despite this discrepancy, the overall roundtrip trajectories realized by the birds allowed for a significantly larger area scanned using olfaction than their respective simulated ones. Hence, rather than maximizing the area scanned at any given point in the foraging trip, our results suggest that the extensive use of crosswinds enables these birds to maximize the area scanned along their whole central place foraging routes.

Many seabirds are well-documented to use their highly developed sense of smell to identify partners and nests (Bonadonna et al. 2004), as well as locate widely distributed food patches over across long distance foraging flights (Nevitt 2008, Nevitt et al. 2008). In fact, *Procellariiformes*

have among the largest olfactory bulbs of birds (Bang & Cobb 1968). This is particularly true for nocturnal seabirds (such as Bulwer's petrels), which have a larger olfactory bulb (relative) size than diurnal species (Healy & Guilford 1990). Our findings strongly support the hypothesis that Bulwer's petrels search for foraging opportunities using their sense of smell, both during day and night, relying on crosswind flight to detect olfactory cues and opportunistically find prey along their route. This may be the key to the ecological success of many other small petrels with similar foraging ecologies, which have global distributions and some of the largest seabird populations on earth. We found that petrels are highly selective for crosswinds not only when realizing fast transit movements, but also when searching for food, consistently for the finer-scale and coarser resolution datasets. Moreover, the petrels exhibit a strikingly similar distribution of wind Δ angle both during day (when visual cues could be used more extensively) and night (when they are instead more limited). Had visual cues been used to detect prey, it would be reasonable to expect the foraging strategies and the movement behavior of petrels to differ considerably between night and day. Further evidence is also provided by the fine-scale movements documented in the 3 min tracks. In some sections, the birds seem to fly crosswind to detect odor filaments, track the smell upwind to the source upon detection, stop to forage and then resume flying along the initial direction (fig. S7 in supplementary material).

4.3 Zig-zag

An emerging property of the Bulwer's petrel tracks is a systematic crosswind zig-zag flight. This zig-zag flight occurs both at the large scale (1 h resolution), when the birds are carrying out fast transit movements, and at a smaller scale (3 min resolution), when they are performing ARS movements upon reaching areas offering good feeding opportunities (fig. 2). The 3 min dataset comprises large sections in which the petrels maintain constant heading, realizing straight crosswind tracks often for the whole duration of the recorded movement burst. Along some tracks, the birds perform sharp turns, changing heading by $\sim 180^\circ$ to fly in the direction that they were coming from. The extensive use of this crosswind zig-zag flight, and its potential importance as an efficient search strategy, is documented here for the first time.

Various anecdotal evidence from at-sea observations and both theoretical (Richardson 2011) and empirical studies (Richardson et al. 2018) suggested that dynamic soaring albatrosses can fly without flapping their wings at virtually any angle with respect to the wind, including directly upwind, by "tacking" like a sail-boat. However, "tacking" implies an overall movement directionality against the wind, involving several sections with an overall upwind heading and smaller turning angles than the sharp turns exhibited by the zig-zagging Bulwer's petrels. Furthermore, as we discussed above, the Bulwer's petrels very rarely engaged in upwind flight and are predicted to attain the lowest ground speed in such conditions. In fact, due to their wing morphology (Spear & Ainley 1997), tacking may be particularly disadvantageous for Bulwer's and other small petrels. Hence, we argue that the systematic zig-zag undertaken by the petrels is underpinned by high selectivity for crosswind during the entire roundtrip, both to maximize the distance travelled and the area scanned olfactorily for foraging opportunities.

5. CONCLUSIONS

Under constant winds, Bulwer's petrels maximize the distance covered and the area scanned using olfaction by performing a systematic crosswind zig-zag flight. When conditions are suitable, petrels also undertake larger clock-wise looping routes, efficiently designed to exploit the higher

wind variability beyond the trade winds belt. The results of this study provide novel elements shedding further light onto the adaptations of dynamic soaring seabirds for the efficient use of stable and predictable winds. Such ecological features make seabirds particularly sensitive to the effects of climate change on the ocean winds. The general atmospheric circulation and particularly the intra-seasonal variability in wind conditions in the subtropics are predicted to be highly impacted by climate change (Shepherd 2014, Miranda et al. 2021). In this context, a thorough understanding of the role played by wind on the movement ecology of seabirds is pivotal, with direct implications for conservation and evidence-based management.

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SUPPLEMENTARY MATERIAL

1. Data Collection

We deployed GPS loggers on incubating Bulwer's petrels from the colonies of Deserta Grande and Selvagem Grande (Madeira, Portugal) during three breeding seasons (June-July of 2015, 2016 and 2021). Tags were programmed to record locations on two schedules. In the first, loggers recorded points every hour; in the second, they recorded relocations every 3 minutes for six hours each day, either from 18 to 24 GMT (in 2016) or from 16 to 22 GMT (in 2021). The latter schedules were adopted to optimize the battery life of the loggers, activating them in hours with and without sun light and when Bulwer's petrels were found to be most active (Dias et al. 2016). To obtain regular trips at 1 h and 3 min resolutions, we linearly interpolated the tracks using the package `adehabitatLT` (Calenge 2016) in R (R Core Team 2019). The extent of interpolation was minimal (less than 2% of the points were imputed). The final dataset comprised 22 tracks at 1 h resolution collected from 22 individuals (in the 2015, 2016 and 2021 breeding seasons) and 64 bouts of relocations at a 3 min resolution collected from 7 individuals (in the 2016 and 2021 breeding seasons).

2. Movement analysis

2.1 Estimate of space use

To quantify the areas most intensely used by the Bulwer's petrels, we generated Kernel Utilization Distributions (UD) based on the 1h resolution tracks, using the `kernelUD` function in the R package `adehabitatHR` (Calenge 2019). The reference system adopted was the geographic coordinate system. The UD bandwidth "h" was set as $1.1 * \text{the maximum step length observed in a 1-hour interval}$ ($h = 50 \text{ km}$). On the geographic grid, this was equivalent to setting $h = 0.49^\circ$. Following the method described in Ventura et al. 2019, we bootstrapped the individual UD's obtaining 100 re-samples, constraining the algorithm to choose at least one individual from each season in each re-sampling iteration. For each re-sampling round, the UD's were added together and normalized so that their sum added up to 1. We obtained 100 bootstrapped, normalized UD's. We then calculated their mean, obtaining an average UD, and the 50% UD contour of the average UD was finally quantified. The space use of the petrels is depicted in figure S1. Based on the 50% UD contour, we identified: a "nearby" high usage area (waters off the Canary islands and West Africa); and a "distant" high usage area (waters off the Azores). If the trips reached the distant area, they were classified as "distant"; conversely, if the trips only overlapped with the "nearby" area, they were classified as "nearby".

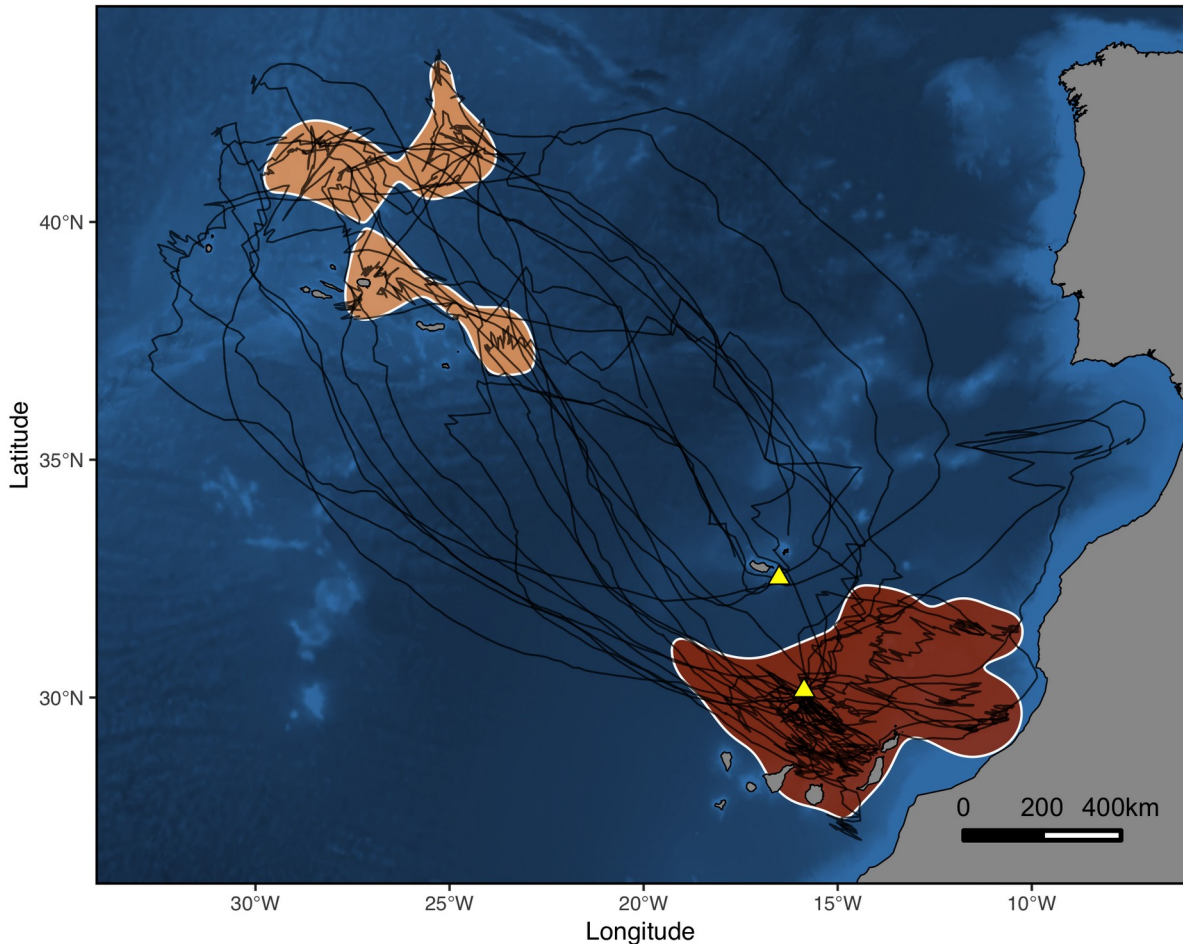


Figure S1 – The "nearby" (dark red) and "distant" (orange) high usage areas, identified as the 50% contour of the Kernel Utilization Distributions.

2.2 Wind use

Bulwer's petrels exhibited a striking preference for crosswinds. In figure 3b in the main text, we compare the Δ angle (i.e. the wind direction relative to the bird bearing) used by the Bulwer's petrels in this study with that measured along the tracks of Cory's shearwaters (*Calonectris borealis*) and Desertas petrels (*Pterodroma deserta*) breeding in the same region (Selvagem Grande and Bugio, respectively). The tracks were linearly interpolated using the R package *adehabitatLT* (Calenge 2016), as described in the main text. The Cory's shearwaters and Desertas petrels tracks were collected at a resolution of 1h and 2h, respectively. The "transit" and "search" behavioral states (see the main text for a thorough description of these two states) along the tracks were identified using hidden Markov models (HMM) from the R package *momentuHMM* (McClintock & Michelot 2018), based on the step length and turning angle data streams. As described in the main text (and below), the intrinsic effect of the tail wind component on the mean parameter of the step length distributions (of both states) was accounted for using a design matrix.

Overall, the Bulwer's petrels showed a clear preference for crosswind flight, both during the transit and the search state (see main text). The wind use of Cory's shearwaters showed a much less pronounced preference for specific wind Δ angle values and the resulting density curves are remarkably broader than those of Bulwer's petrels (figure 3b in the main text). Cory's shearwaters are diurnal predators feeding on epipelagic prey, showing foraging site fidelity to predictably

productive areas. As we discuss in the main text, Cory's shearwaters do not exhibit a clear preference for crosswind flight potentially due to the advantages of commuting to these rich areas and thereby focussing the food search, despite a sub-optimal wind use. Moreover, during their search, the shearwaters may further deviate from crosswind flight by visual pursue of external cues regardless of the wind conditions experienced, for instance by heading towards other foraging individuals or fishing vessels. The Desertas petrels, instead, most intensely used quartering tail winds $< 90^\circ$ (flying at $\sim 60^\circ$ when in "transit", figure 3b in the main text). These birds travelled beyond the northern edge of the trade winds belt. As described in Ventura et al. 2020 and in the main text, they exploit the wind variability beyond the trade winds belt to carry out fast, long looping routes, traveling at an advantageous angle with respect to the wind during their entire round route.

2.3. State space modelling

The behavioral states of Bulwer's petrels along the tracks were identified using Hidden Markov models (HMMs). HMMs are time series models in which one or more observed data-streams (such as the distance travelled and the change of movement direction between consecutive relocations, i.e. the "step length" and the "turning angle", respectively) are fit to state-dependent probability distributions, with different parameter sets describing movement representing different latent or "hidden" states. This state sequence is then inferred by fitting the model to the empirical GPS relocations assuming that the movement dynamics are driven by a Markov process (Zucchini & MacDonald 2009). The most likely state sequence is then inferred using the Viterbi algorithm (Zucchini & MacDonald 2009). We assumed that, along the 1 h resolution tracks, the petrels were in one of two behavioral states: "transit", in which the underlying drive is to move at high speed in a persistent heading; or "search", in which the drive is to search for food upon entering a foraging patch. Conventionally, the transit state is assumed to be characterized by high speed and high movement directionality, whereas slower movement with more variable turning angles are indicative of the search state (Patterson et al. 2008). Nevertheless, the Bulwer's petrel tracks were characterized by few, sharp turns between sections at high speed and high movement directionality. Hence, HMMs were fit only to the step length data, as the inclusion of turning angles led to misclassification of the sharp turning points (i.e. the vertices of the zig-zagging sections, see main text) as search locations. In the 3 min resolution tracks, we assumed that the petrels were in one of these three states: "in flight", when the birds spent the entire move step flying; "on water", when the animals spent the entire move step sitting on the water surface to ingest and process food or rest; and "mixed", an intermediate state in which the animals spent part of the step in flight and part on the water, indicative of foraging attempts. HMM models fitted to the 3 min tracks also used only the step length data and not turning angles. Different step lengths between observations reflect the true behavioral state of the animal, in which longer steps are indicative of a transit state, whereas a slower flight with shorter steps represents search sections. However, the step length is also intrinsically dependent on the tail wind component ("TWC", calculated as in Dell'Arciccia et al. 2018), which quantifies the wind speed component in the direction of flight. Hence, for both the 1 h and 3 min resolution tracks, within the HMM modeling formulation we modeled the mean parameter of the state-dependent probability distribution of step length as a function of TWC. In so doing, using the DM (design-matrix) argument from the `momentuHMM` package, we accounted for the TWC effect on the mean parameter of the state-dependent step length distributions. The most likely sequence of hidden states was then computed using the Viterbi algorithm (Zucchini & MacDonald 2009).

3. Wind and odor plume model

3.1 Wind model

We hereby present the results of the wind model based on the 3 min resolution tracks. The analysis focussed on the locations classified as "in flight" in the 3min resolution tracks, as we assumed that, when the birds were in this state, the relationship between wind and speed would not be biased by other activities performed when searching or resting. We used generalised additive mixed effect modelling (GAMM) from the `mgcv` package (Wood 2006) in R to quantify the effect of Δ angle, wind intensity and their interaction on the ground speed of the petrels. The following gaussian "wind model" GAMM was fit to the data:

step length $\sim f(\Delta\text{angle}) + f(\text{wind intensity}), \text{corAR}_1(\text{Timestep}|\text{ID})$.

As also described in the main text, the functions f are cubic regression splines with shrinkage. The model included the tensor product interaction between variables and the residual autoregressive AR_1 correlation structure to account for both temporal autocorrelation and for the dependency between points collected on the same animal. The best set of candidate variables to retain in the wind model was selected based on AIC.

The results of this wind model are in line with those yielded by the model fitted to the 1h resolution data. The wind model based on the finer 3min resolution tracks retained Δ angle and wind intensity but not their interaction (unlike the model based on the 1h resolution data) as significant explanatory variables. The model predicted a decrease in ground speed as the Δ angle shifted from tail winds to head winds (figure S2).

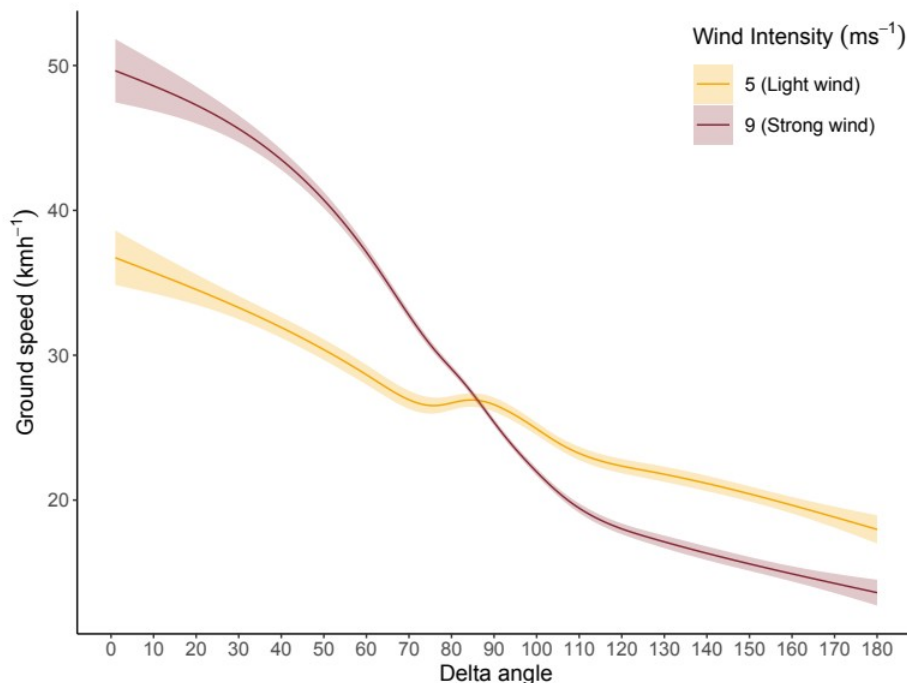


Figure S2 – Results of the generalized additive mixed effect "wind model", fitted to the "in flight" sections of the 3min resolution trips. The 95% confidence interval is represented by the shaded areas. For visualization purpose, the predicted effect of Δ angle on ground speed (km/h) was calculated for light (5m/s) and strong (9 m/s) winds.

3.2 Odor plume model and olfactory bandwidth

Gaussian plume models (Holzbecher 2012) (referred to as "odor plume model") were built to analytically describe the wind-driven advection of odor plumes. We followed equation 16.22 and figure 16.6 in Holzbecher (2012) and developed the odor plume model assuming: constant emission rate, diffusivity on the y- and z-axis of $1000 \text{ m}^2\text{s}^{-1}$; constant decay; and advection driven by a constant and uniform wind. As described in the main text, the threshold distance of smell detection was computed assuming that birds could detect the smell when it decayed to $2 \cdot 10^{-4}$ of the intensity estimated at a distance of 1 m from the source. A set of odor plume models and resulting oval smell detection contour lines were generated with wind intensities ranging from 1 to 15 ms^{-1} .

We used predictions from the odor plume model (the smell detection contour lines for a given wind intensity) and from the wind model (the predicted ground speed attained by the bird flying at a given Δ angle and wind intensity) to calculate two key quantities: the "olfactory bandwidth" and the theoretical area (km^2) olfactorily scanned (more thoroughly described in the main text).

The "olfactory bandwidth" (i.e. the maximum distance from the source at which the birds are predicted to detect a smell) was calculated for each value of Δ angle and wind intensity applying trigonometric formulae. To do so, on each dispersal raster obtained for a given wind intensity, we simulated a bird flying at a Δ angle of 10° to 170° . For each Δ angle and wind intensity considered, we drew the flight trajectory tangent to the oval smell detection contour (refer to fig. 1 in the main text for a visual representation). For each Δ angle and wind intensity values specified, we obtained a right triangle delimited by: the hypotenuse, along the major axis of the oval smell detection contour (O'I' and OI for Δ angle of 10° and 80° respectively, fig. 1 in the main text); the cathetus "C1" adjacent to Δ angle, given by the flight trajectory tangent to the oval smell detection contour (A'I' and AI, adjacent to the Δ angle of 10° and 80° in fig. 1 in the main text); and the cathetus "C2" opposite to Δ angle, i.e. the perpendicular line connecting the smell source to C1 (OA' and OA, fig. 1 in the main text). After finding the intersection point between the major axis of the oval smell detection contour and the tangent flight trajectory (I' and I for Δ angle of 10° and 80° respectively, fig. 1 in the main text) we extracted the hypotenuse length and calculated the length of C2 by applying the trigonometric formula:

$$C2 = \text{hypotenuse} * \text{Sin}(\Delta\text{angle}).$$

The cathetus C2 thus calculated was the olfactory bandwidth, i.e. the maximum distance from the source at which the birds are predicted to detect a smell, for each value of Δ angle and wind intensity.

The odor plume model showed that, as the wind intensity increased, the oval representing the smell detection contour became more and more stretched along the major axis (figure S3). Nevertheless, for all wind intensities considered, the olfactory bandwidth peaked at a Δ angle value = 90° (figure S4).

We carried out a sensitivity analysis by choosing a range of realistic diffusivity parameter values (800 to $1200 \text{ m}^2\text{s}^{-1}$), and formulating the odor plume model as described above. Furthermore, we tested the sensitivity of our results to changes in the definition of the smell detection contour line, computing it as the isoline where the odor concentration decayed to $1 \cdot 10^{-4}$ and $5 \cdot 10^{-4}$ of the concentration estimated at a distance of 1 m. For all diffusivities and smell detection contours considered, the olfactory bandwidth remained highest for Δ angle = 90° . Additionally, while (trivially) the size of the area scanned changed for the different smell detection contours

considered, the diffusivities chosen had a lesser impact on the size of the area scanned. Moreover, despite the changes in absolute area scanned size, the results obtained on the relationship between wind Δ angle, wind intensity and area scanned (described in the main text) were robust to the parameter specification (figure S5).

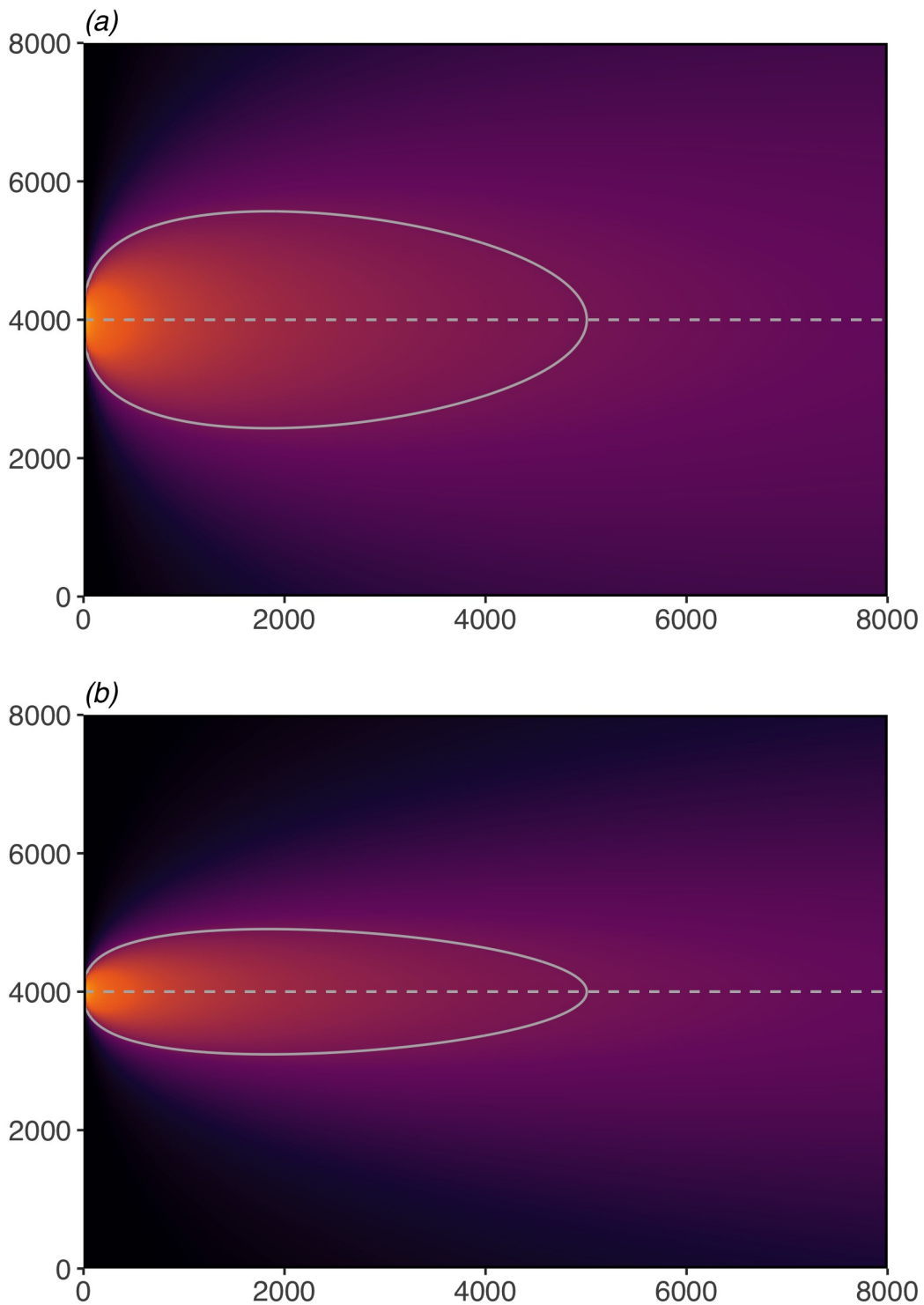


Figure S3 – Grid showing the oval smell detection contour line generated by the Gaussian plume "odor plume model". The oval contour line was calculated as the isoline where the intensity of the smell decayed

to 2×10^{-4} of the intensity measured at a distance of 1 m from the source. As the wind intensity increased from 3 m s^{-1} (a) to 9 m s^{-1} (b), the smell detection contour became more stretched along the major axis.

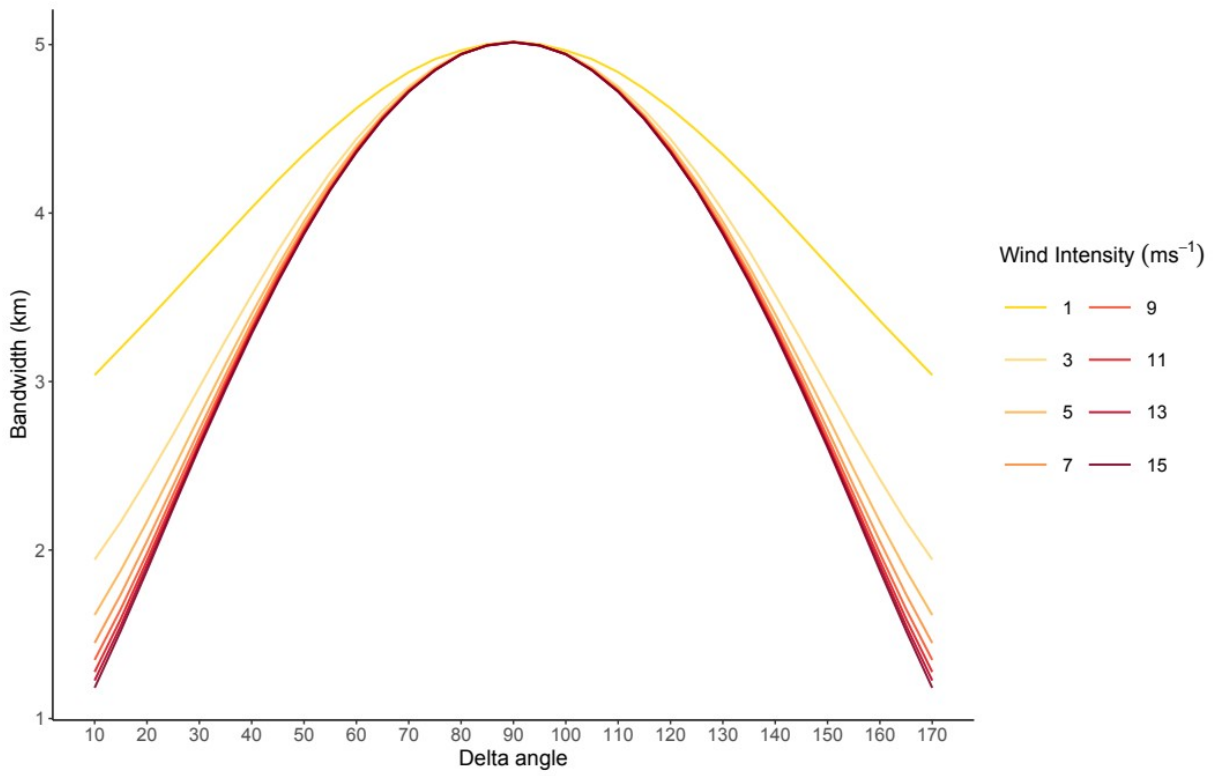


Figure S4 – The relationship between Δ angle and olfactory bandwidth predicted by the odor plume model, for different wind intensities and given a diffusivity of $1000 \text{ m}^2 \text{ s}^{-1}$. The bandwidth is maximized at Δ angle = 90° .

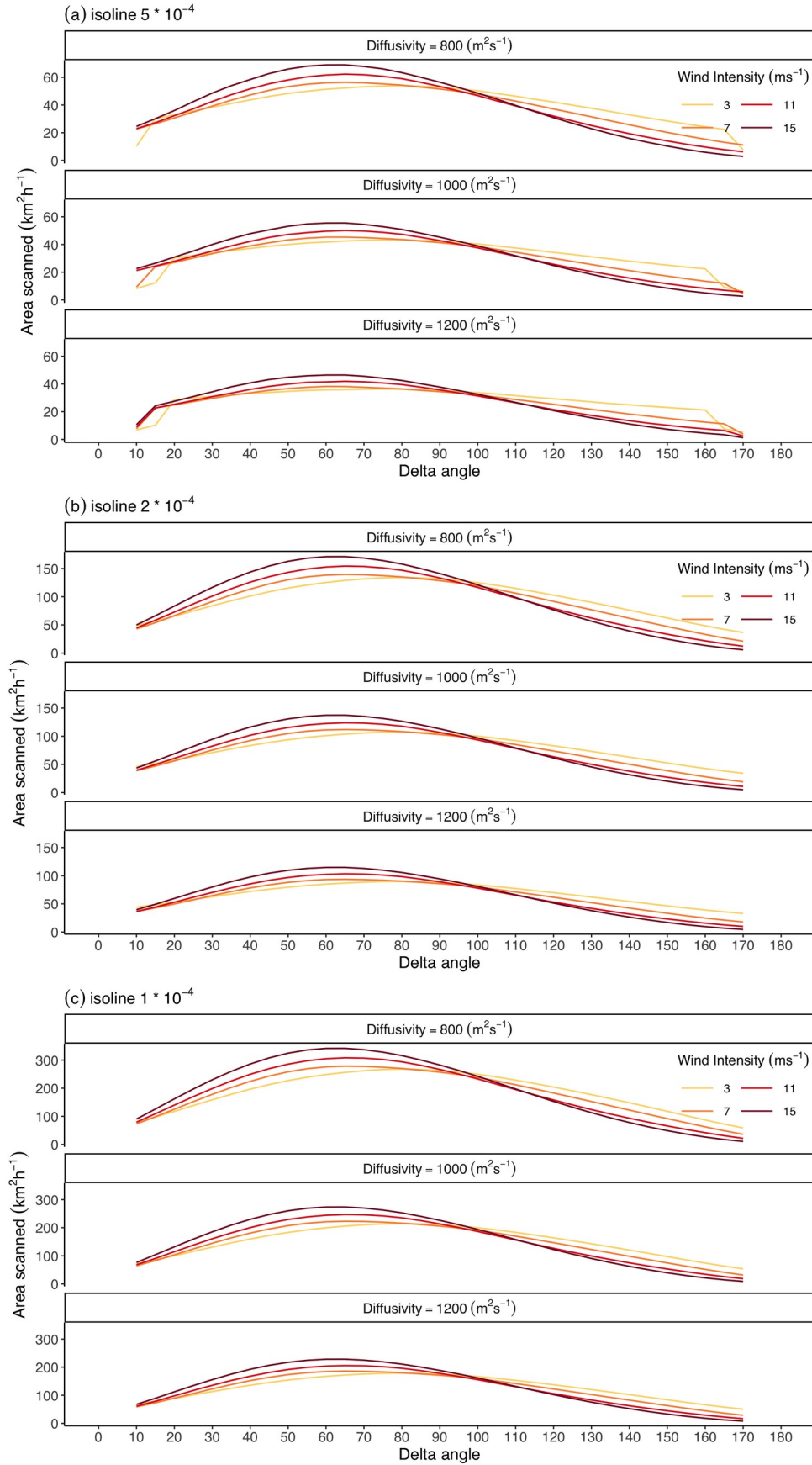


Figure S5 – The odor plume model sensitivity analysis, carried out by choosing a range of realistic diffusivity parameter values (800 to 1200 m²s⁻¹), and by computing the smell detection contour line as the

isoline where the odor concentration decayed to $5 \cdot 10^{-4}$ (panel a), $2 \cdot 10^{-4}$ (panel b) and $1 \cdot 10^{-4}$ (panel c) of the concentration estimated at a distance of 1 m. Despite the differences in absolute area scanned size, the relationship between wind Δ angle, wind intensity and area scanned is robust to the parameters specification.

4. Track simulation

A simulation framework was used to investigate whether the 1h resolution tracks enabled the birds to: maximize their speed and cover the most distance in the shortest time; and maximize the area scanned using olfaction along their route. For each track, we simulated 100 "random" and 100 "rotated" tracks. Following the methodology presented in Ventura et al. 2020, only the transit bouts of the tracks were considered. The last point of each transit section interrupted by search locations was thus connected to the first point of the subsequent transit bout by a beeline segment. These connecting segments were retained to preserve the trip configuration and carry out the simulation, but their duration and area scanned were discarded from the calculation of the final trip metrics. The values yielded by the simulation framework therefore only refer to the 'transit' section of the tracks, rather than to the overall routes.

To simulate each random trip, we divided the real trip into two sections: from the colony to the most distant foraging location and vice versa. Within each of these two sections all the segments between the GPS relocations were randomly reshuffled. To generate the rotated trips, we used the `adehabitatLT` package (Calenge 2016) to design a random rotate-shift model centered on the colony location. Thus, the simulated tracks (both random and rotated) were equivalent (i.e. covering the same distance), but along these routes the birds used different wind Δ angle than the real tracks. The duration of each simulated trip was calculated as follows. The start location of the real and simulated trip shared the same timestamp. From this start point "s", we calculated the time needed for the bird to travel to the next point "s + 1" based on the ground speed predicted by the wind model for the given the wind conditions (Δ angle and wind intensity) experienced at "s". The time of arrival at "s + 1" and the local wind conditions at that time were calculated. This protocol was repeated for all locations along the simulated trip and its cumulative duration was calculated and compared to the duration of the respective real trip.

Together with the cumulative duration of the simulated tracks, we also calculated the area scanned by the birds along the real track and the respective random and rotated trips. For each timestep along real and simulated tracks: the Δ angle and wind intensity values were extracted; the olfactory bandwidth was estimated based on the predictions of the odor plume model; the observed step length was multiplied the olfactory bandwidth, thus obtaining the area scanned using olfaction. The cumulative area scanned throughout real and respective simulated trips was finally calculated.

As we outline in the main text, the real tracks realized by the transiting petrels were significantly faster than random and rotated trips. The real transit bouts were, on average, 175h and 211h (i.e. 136% and 164%) faster than the transit bouts in the respective random and rotated trips (figure S6). Moreover, the area scanned throughout the real trips was significantly wider than the area scanned along the random and rotated tracks. The area scanned along the real trips was on average 646 km² and 1304 km² (i.e. 5% and 11%) wider than the area scanned along the respective random and rotated trips (figure S6).

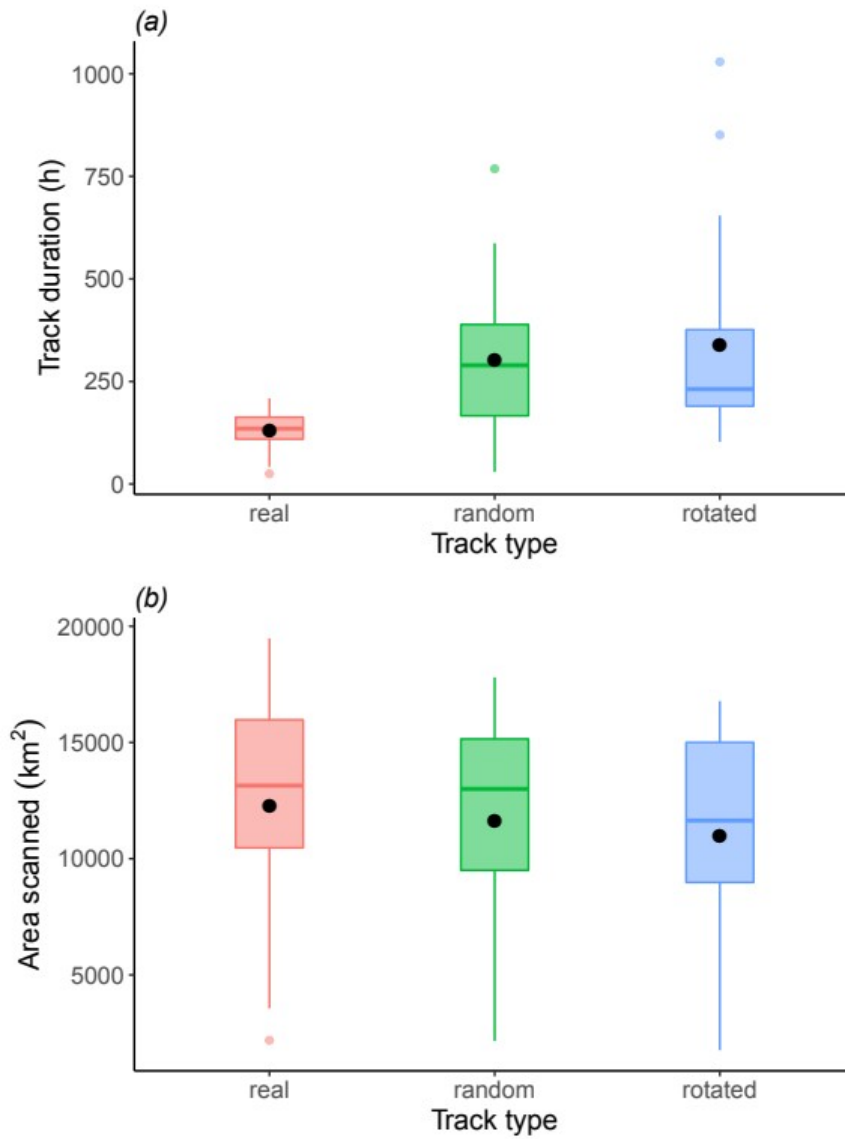


Figure S6 – Boxplot showing (a) the duration (in hours) and (b) the area scanned (in km²) of the real, random and rotated trips. The black circle represents the mean.

5. Examples of olfactory foraging along the 3 min resolution tracks

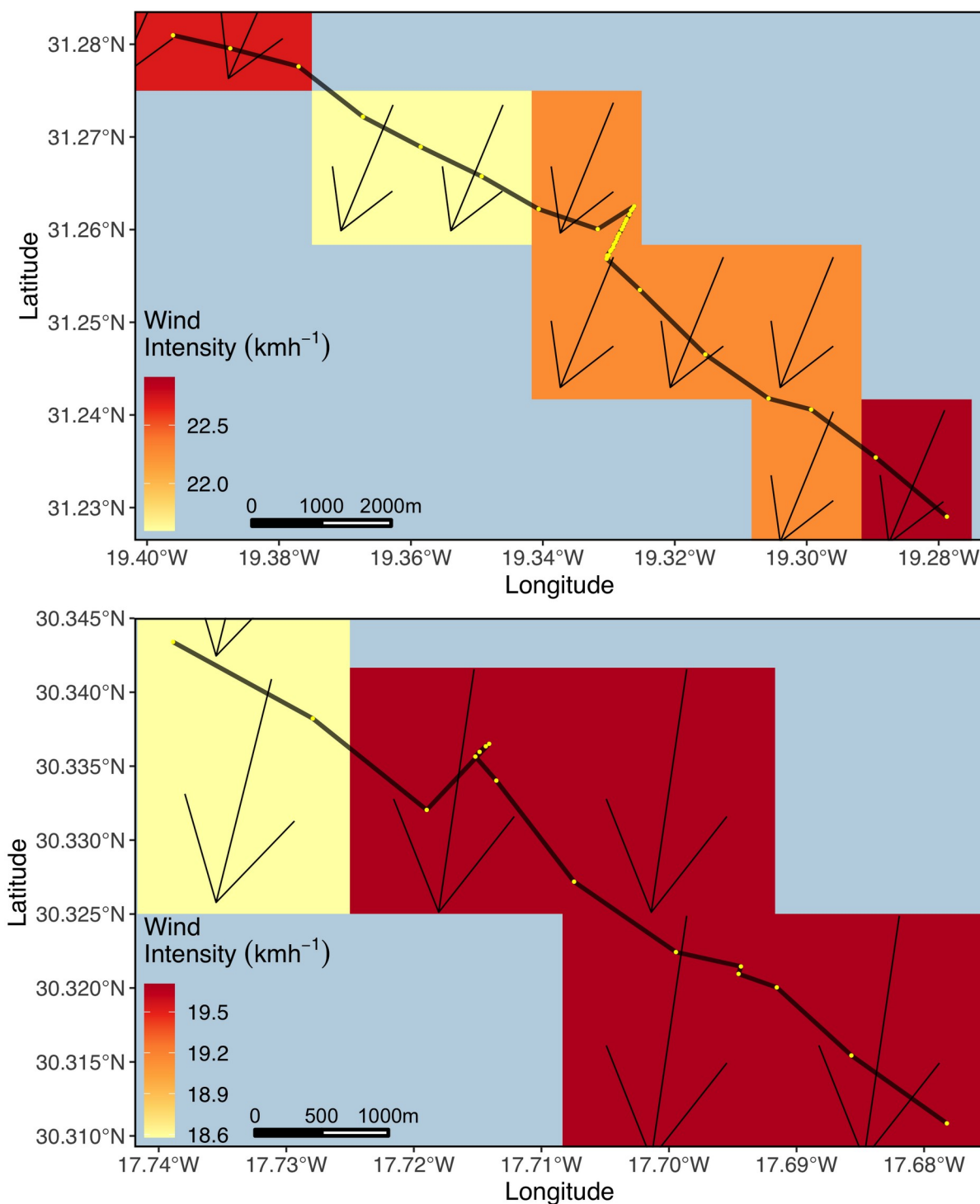


Figure S7 – Two visual examples indicative of the occurrence of olfactory foraging along the 3min resolution tracks. In both examples, the petrels are engaging in crosswind flight, at night, moving from northwest to southeast. In two sections of the movement bouts (one per panel), the birds seem to: track the odor filaments upwind for approximately 500m; engage in foraging and sit on the surface of the water to process food (indicated by the sections in which the points are clustered together); finally, resume flying along the initial direction of movement. The arrows represent the real-time wind conditions experienced along the tracks, whereas the yellow points are the GPS relocations.

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CHAPTER 7

GENERAL DISCUSSION

This thesis provides novel insight into the pathways through which oceanographic processes and wind shape the demography, population dynamics, movement and spatial distribution of procellariiform seabirds. In Chapter 2, we investigate the environmental drivers of productivity and survival rates of the black-browed albatross. Our integrated modelling framework provides among the first quantitative estimates of the high sensitivity of the population to the survival of juveniles, highlighting the importance of the cryptic (and traditionally overlooked) sub-adult stages, which make up approximately half of the total population. Furthermore, our findings show that, while the population productivity was affected by wind and local oceanography, survival was influenced by deeper ecosystem changes acting at larger spatio-temporal scales. As we describe in Chapter 3, part of the fluctuation in breeding success was not explained by environmentally-driven food regulation and chick malnutrition. By documenting the existence of spatio-temporal patterns in albatross chick mortality events, our work strongly suggests the prevalence of an unidentified infectious disease widely affecting the black-browed albatross breeding success in the Falklands. In Chapter 4, we focus on mate choice and divorce in the black-browed albatross. For the first time, we found a direct effect of oceanographic conditions on the prevalence of divorce in a socially monogamous population. Chapter 5 and Chapter 6 focus on the foraging movements and use of wind of the Desertas petrel and the Bulwer's petrel. Desertas petrels consistently flew at the angle relative to the wind that maximised their speed throughout their round-trips, carrying out some of the longest foraging trips known in any animal. Bulwer's petrels, instead, exhibited a striking selectivity for crosswinds, orienting orthogonally to the prevailing trade winds. Under stable winds, we showed that this strategy enabled them to maximise both the round-trip distance covered and their olfactory search efficiency.

In the following sections, I discuss to what extent our work contributes to an improved understanding of the population and spatial ecology of *Procellariiformes*. I also describe how, while addressing fundamental ecological questions, this thesis provides valuable and relevant insight for seabird conservation. Finally, in the concluding section, I outline the pathways for future research to address the new questions raised by this work.

Effects of wind and oceanography on seabird population processes

Wind and physical oceanographic phenomena (e.g. the convergence or divergence of water masses or the interaction between water currents and bathymetry) promote physical forcing of deeper, cooler and nutrient-rich waters to the ocean surface. The enhanced water mixing, in turn, determines a higher availability of nutrients in the photic zone, supporting a higher primary and secondary production, and also concentrating prey for seabirds by advecting and aggregating biomass to the surface (Mann & Lazier 2013). Due to high survival and low predation pressure, the natural regulation of seabird populations is thought to be driven primarily by this environmentally driven regulation of food supply (Cury et al. 2011). Strong evidence for the bottom-up regulation of seabird populations is provided by our demographic work on the black-browed albatross, which exhibits diagnostic population responses to changes in oceanographic and wind conditions. Furthermore, in line with the predictions of the life history theory, environmental changes mainly acted upon the population breeding processes of the long-lived black-browed albatross, whereas their survival remained generally constant.

Our demographic study showed that the black-browed albatross population was sensitive to ecosystem changes in a range of time scales. The reproduction performance of seabirds responds to changes in environmental conditions on a scale of months (Weimerskirch et al. 2001, 2012, Quillfeldt et al. 2007). However, deeper changes affecting the ecosystem structure and occurring across multiple years and over a large spatial domain can ultimately have repercussions on survival (Descamps et al. 2016, Abadi et al. 2017). Thus, in the context of the current biodiversity crisis, our work provides further support to the use of seabirds as bioindicators of the health of the global ocean (Boyd & Murray 2001, Sergio et al. 2008). Our study shows that the "sentinel" role of seabird populations can provide critical insight into ecosystem changes occurring at different scales (Velarde et al. 2019). For instance, monitoring the breeding processes of seabirds may provide quick, diagnostic responses useful for ecosystem-based management approaches. Changes in survival, likely concurrently exhibited by several top-predator populations, may be useful to signal the occurrence of structural ecosystem changes and to obtain important insight for a more process-based understanding of the effects of climate change on marine ecosystems.

The effect of wind on seabird demography is not only limited to the increased *availability* of prey. Wind shapes the *accessibility* of foraging patches by determining the cost of flight for dynamic soaring seabirds, particularly so during the breeding season, when they have to periodically return to their colony. In recent years, it has become increasingly evident that, by shaping their flight efficiency and foraging performance, wind is a key driver of seabird demographic processes (Weimerskirch et al. 2012, Thorne et al. 2016). For instance, as a result of the increasing intensity of the westerly winds in the Southern Indian Ocean, the travel speed of foraging wandering albatrosses (*Diomedea exulans*) has increased, the duration of their foraging trips has decreased, and their breeding success has improved (Weimerskirch et al. 2012). The positive effect of increased wind intensities on albatrosses is perhaps unsurprising, since they can sustain energy efficient flight at virtually any angle relative to the wind. A tendon "shoulder lock" allows albatrosses to hold their wings in position despite the action of wind from below, further improving their soaring performance under strong winds (Pennycuik 1982). An extreme example is provided by a tracked grey-headed albatross (*Thalassarche chrysostoma*), which used the strong winds of an Antarctic storm to travel at a mean ground speed of over 120 km h^{-1} for approximately 10 h, still managing to successfully capture prey despite the storminess of the sea (Catry et al. 2004). However, these wind-driven effects on seabird foraging performance and population processes have been mostly documented in large albatrosses. In smaller seabirds increased wind intensities may entail a higher cost of flight, resulting in lower foraging performances and having a negative impact on population processes. However, at present this remains largely unknown.

Despite being poorly understood, sub-adults life history stages play a fundamental role in seabird population dynamics. The importance of sub-adults can perhaps be best demonstrated by the practical example of the massacres of Cory's shearwaters that took place in 1975-1976 on Selvagem Grande, Portugal. In response to the designation of the island as a Nature Reserve, Spanish and Portuguese fishermen deliberately killed thousands of Cory's shearwaters, both adults and nestlings, causing a major population collapse and leaving as few as 64 chicks alive on land (Granadeiro et al. 2006). However, a large number of sub-adults and non-breeding birds were at sea during the massacres (Mougin et al. 2000). As they progressively recruited in their natal colony in subsequent years, the breeding population gradually recovered and, despite being far from its historic abundance, Selvagem Grande is now home to the largest Cory's shearwater colony in the world (Granadeiro et al. 2006). The current gaps of knowledge on the "lost years" of immaturity represent an evident, major factor hindering our understanding of seabird population

processes and the development of comprehensive conservation measures (Hazen et al. 2012). Our albatross demographic study provided among the first quantitative evidence of the importance of sub-adult age classes to the population dynamics. These results have clear conservation implications and have the potential to serve as quantitative basis to develop integrated evaluations of seabird population dynamics, distribution and threats (Clay et al. 2019b, Carneiro et al. 2020).

The pivotal importance of longitudinal datasets to investigate the environmental drivers of seabird demographic processes has long been recognised (Jenouvrier 2013). Long-term, ongoing integrated monitoring projects (Greenwood et al. 1993) continue to yield seabird population counts, individual based capture-mark-recapture datasets and productivity data. However, until very recently, there has been an evident mismatch between the development of statistical modelling approaches and the ever increasing availability of data (Zipkin & Saunders 2018). In this context, our demographic work represents an important contribution from a methodological perspective. Our study provides a proof of concept of the great potential that integrated population models have in quantifying the rates shaping the dynamics of the whole population, including the cryptic sub-adult stages. Given the flexibility of this modelling approach and the availability of high resolution datasets for many seabird populations, integrated population models promise to be a critical tool for the study of seabird population ecology in the context of global change (Véran & Lebreton 2008, Schaub & Abadi 2011, Zipkin & Saunders 2018).

As described above, fluctuations in oceanographic conditions largely affected albatross breeding processes and reproductive performance. Increases in sea surface temperatures were negatively correlated with the yearly body mass of albatross chicks, further indicating a lower availability of food in seasons characterised by warmer waters. Nevertheless, malnutrition and bottom-up food availability was not the primary driver of albatross chick mortality events unrelated to predation. Rather, the occurrence of spatio-temporally aggregated patterns of mortality strongly suggests the prevalence of an unidentified disease, with a variable impact on the population breeding success in different years. The widespread occurrence of clustered mortality events in multiple albatross colonies and the similar symptoms exhibited by most deceased chicks suggest that this disease is widespread across the colonies in the Falkland archipelago. However, both the pathogenic agent involved and the means of contagion are unknown and can only be understood through appropriate histopathological analyses (Gamble et al. 2019, 2020), which is a conservation priority given the global importance of the Falklands black-browed albatross population.

The oceanographic processes regulating food availability do not affect only the breeding rate and breeding success of socially monogamous populations. By focussing on the reproductive performance of albatross breeding pairs followed for nearly two decades, our work sheds new light on a previously hypothesised (Blondel et al. 2000), but never empirically documented habitat-mediated pathway through which environmental changes impact the breeding processes of a socially monogamous population. For the first time we found that, regardless of their previous breeding performance, increases in sea surface temperatures lead to an increase in the prevalence of divorce. This finding highlights the existence of direct pathways linking environmental changes and divorce in monogamous populations. Whether environmentally-driven divorces also occur in smaller threatened populations is currently unknown, and may represent a matter of conservation concern. Moreover, the interaction between environmental conditions, population size and mate selectivity is poorly understood. For instance, new evidence suggests that smaller populations may exhibit a decreased selectivity for mates (Bried et al. 2021).

However, whether the effects of the environment on mate choice and breeding processes are different for populations of different sizes is not known at present. Given its flexibility and wide applicability to other study systems, the state-space modelling formulation developed in our work has the potential to successfully address these questions.

Wind, a key driver of seabird spatial ecology

In the context of the optimal foraging theory predictions, the foraging movements realised by the Desertas petrels and Bulwer's petrels challenged our intuitive understanding of the costs and benefits underpinning the movement strategies adopted. When looking at the ocean-wide looping trips of the Desertas petrels, one cannot help but wonder why these petrels choose to embark on some of the longest foraging trips documented in the animal kingdom, particularly given the proximity of their colony to the productive waters of the Canary Current (Wynn & Knefelkamp 2004, Camphuysen & der Meer 2005, Eckert 2006). Bulwer's petrels, instead, carried out large zig zag movements, covering thousands of kilometres, often alternating sections of high movement directionality with sharp turns to fly in the direction that they were coming from. In line with both theoretical and empirical bodies of work (Weimerskirch et al. 2000, Wakefield et al. 2009, Alerstam et al. 2019), our research shows that the key driver underpinning the observed flight patterns is the wind, which deeply shapes the spatial and foraging ecology of procellariiform seabirds.

The model organisms investigated in our work are specialised predators of mesopelagic prey, a feature shared by most small and medium sized procellariiform seabirds inhabiting tropical and subtropical regions (Spear et al. 2007). Mesopelagic fishes and invertebrates represent a major source of biomass in the marine domain. However, the feeding opportunities for seabirds feeding on mesopelagic fauna is constrained by the surface availability of their prey, which is highly variable throughout the diurnal cycle – as they display diel vertical migrations – and highly heterogeneous in space – as they are much more abundant in open oceanic waters where they are the dominant components of the food webs (Gjørseter & Kawaguchi 1980, Nybakken 2001, Pusch et al. 2004). In line with the findings of recent studies (Clay et al. 2019a), our work shows that seabirds feeding on such an ephemeral food resource rely on a foraging strategy aimed at maximising the probability of prey encounter by covering as much distance as possible. This maximisation of distance covered in search of prey is achieved by dynamic soaring seabirds with an extremely efficient use of wind.

To maximise their travelling speed and minimise the energetic cost of locomotion, dynamic soaring seabirds fly orienting themselves at an angle relative to the wind that maximises their travelling speed and minimise their energy expenditure (Weimerskirch et al. 2000, Sakamoto et al. 2013). The optimal angle relative to the wind is intrinsically dictated by species-specific anatomical and morphological characteristics (Spear & Ainley 1997). For instance, due to the different size and wing morphology, our study shows that the instantaneous ground speed of Desertas petrels is predicted to be highest with side winds (at an angle of $\sim 50^\circ$), whereas the smaller Bulwer's petrels fly the fastest with more quartering-tail winds (between 30° and 40°). However, due to the central place constraint, maximising the instantaneous ground speed is often not the most efficient strategy to maximise the round-trip distance covered. In fact, in order to maximise the distance covered seabirds not only need to be capable of refining their trajectories based on the real-time wind conditions; crucially, they also need to design the most efficient routes considering both the outbound and homebound sections of their trip (Alerstam et al.

2019). Our work shows that seabirds are able to do so thanks to *a priori* knowledge of the regional winds.

Upon departure from their colony, Bulwer's petrels in the stable trade winds do not use the wind angle that maximises their instantaneous speed, as that would entail the high costs of returning to the colony with headwinds. Rather, they fly with crosswinds (blowing orthogonally to their direction of movement), which we demonstrate to be the optimal strategy to maximise the round-trip distance covered under stable winds, a result that is in line with theoretical predictions (Alerstam et al. 2019). Moreover, our results show that the use of crosswinds also enabled Bulwer's petrels to maximise their olfactory search efficiency throughout their whole route. The wind-driven advection and transport of odour plumes of foraging opportunities (Nevitt et al. 2008) may be particularly relevant for Bulwer's petrels and other nocturnal seabirds, likely further underpinning their selectivity for crosswinds. The larger and faster Desertas petrels, instead, engaged in foraging movements that took them beyond the trade winds belt. Thus, they could exploit the higher variability in wind conditions and consistently select their preferred angle with respect to the wind (i.e. the angle that maximised their instantaneous speed) throughout the round trip, in turn enabling them to carry out long, fast looping routes.

The overall picture emerging from our research is that dynamic soaring procellariiform seabirds are supremely adapted to make efficient use of wind, which is key to sustaining their hypermobile life style. Their foraging movements are not only dictated by the effects of wind on their instantaneous flight efficiency, but rather are the product of a complex interplay between the species' foraging ecology and extrinsic environmental drivers (such the variability of wind conditions and the predictability of prey distribution). Crucially, our work strongly suggests that these seabirds have an impressive knowledge of the regional winds and are capable of planning their foraging trips with an expectation of future wind conditions and costs of flight to return to the colony.

Collectively, our findings reveal the key role of wind for subsidising the foraging movements of seabirds. Due to their reliance on winds, seabirds are particularly sensitive to the forecasted changes in global atmospheric circulation and regional winds brought by climate change (Shepherd 2014). However, the predicted effects of these changes on seabird spatial ecology is still poorly understood and requires further investigation. From a methodological perspective, our state-space models and simulation framework allow fundamental ecological questions to be addressed using a hypothetico-deductive approach. This framework can be implemented on other study systems and has the potential to significantly improve our understanding of seabird spatial ecology. From an applied perspective, this research provides further evidence of the real extent of the pelagic distribution of seabirds, focussing on two species poorly represented in the literature. It is increasingly evident that the success of the management and conservation of seabird populations relies on the development of international initiatives, in order to encompass their ocean-wide distribution often extending to the high seas beyond national jurisdictions (Beal et al. 2021).

Avenues for future research

By addressing important questions on the population and spatial ecology of seabirds, my thesis also opens up further questions and highlights potential avenues for future research. The next logical step stemming from this work is to apply the methods developed here to multiple seabird populations. For instance, long-term datasets for the black-browed albatross are available for several locations in the South Atlantic and Southern Indian Ocean. In different colonies,

albatrosses face a highly variable set of environmental conditions and show contrasting population trajectories. This variability in population trends and environmental conditions will be critical for a mechanistic-based understanding of the environmental drivers affecting their demographic processes at various spatial and temporal scales. Furthermore, by investigating mate-choice in different seabird populations, it will be possible to understand whether the effects of the environment on divorce are different for populations with different sizes and facing different environmental conditions.

Similarly, broadening the analytical lens of this research to investigate the spatial and movement ecology of other dynamic soaring seabird populations will be critical for shedding light on the many questions that remain unanswered. On a finer-scale, it is still poorly understood how the different species specific morphological and anatomic adaptations affect the optimal orientation angle with respect to the winds and the flight efficiency. Furthermore, our work shows that the large scale movement patterns of seabirds are driven by both intrinsic (e.g. body mass and wing anatomy) and extrinsic (e.g. wind) characteristics. Hence, to understand the mechanisms driving the central place foraging trips regulation in seabirds, it will be fundamental to carry out tracking studies targeting populations with different intrinsic characteristics, and in colonies experiencing different wind regimes.

Lastly, our work sheds light on various pathways through which changes in wind and oceanographic conditions affect seabird populations. In light of the impact of climate change on the oceans and its accelerating pace (IPCC 2019), measuring and understanding such pathways is critical for forecasting the future viability of marine populations (Jenouvrier 2013). However, forecasting ecology approaches for predicting how populations will adjust to environmental change are still underdeveloped (Iles & Jenouvrier 2019). In this context, the state-of-the-art statistical methodologies developed in this thesis have the potential to address this shortcoming. By broadening our analysis to multiple populations exhibiting different trends and facing different environmental conditions, it will be possible to develop transferrable models to predict how seabird populations will respond to changes and perform in new environments. Given the ever increasing availability of data and societal demand for reliable ecological forecasts, such an approach promises to provide critical insight for conservation and resource management.

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